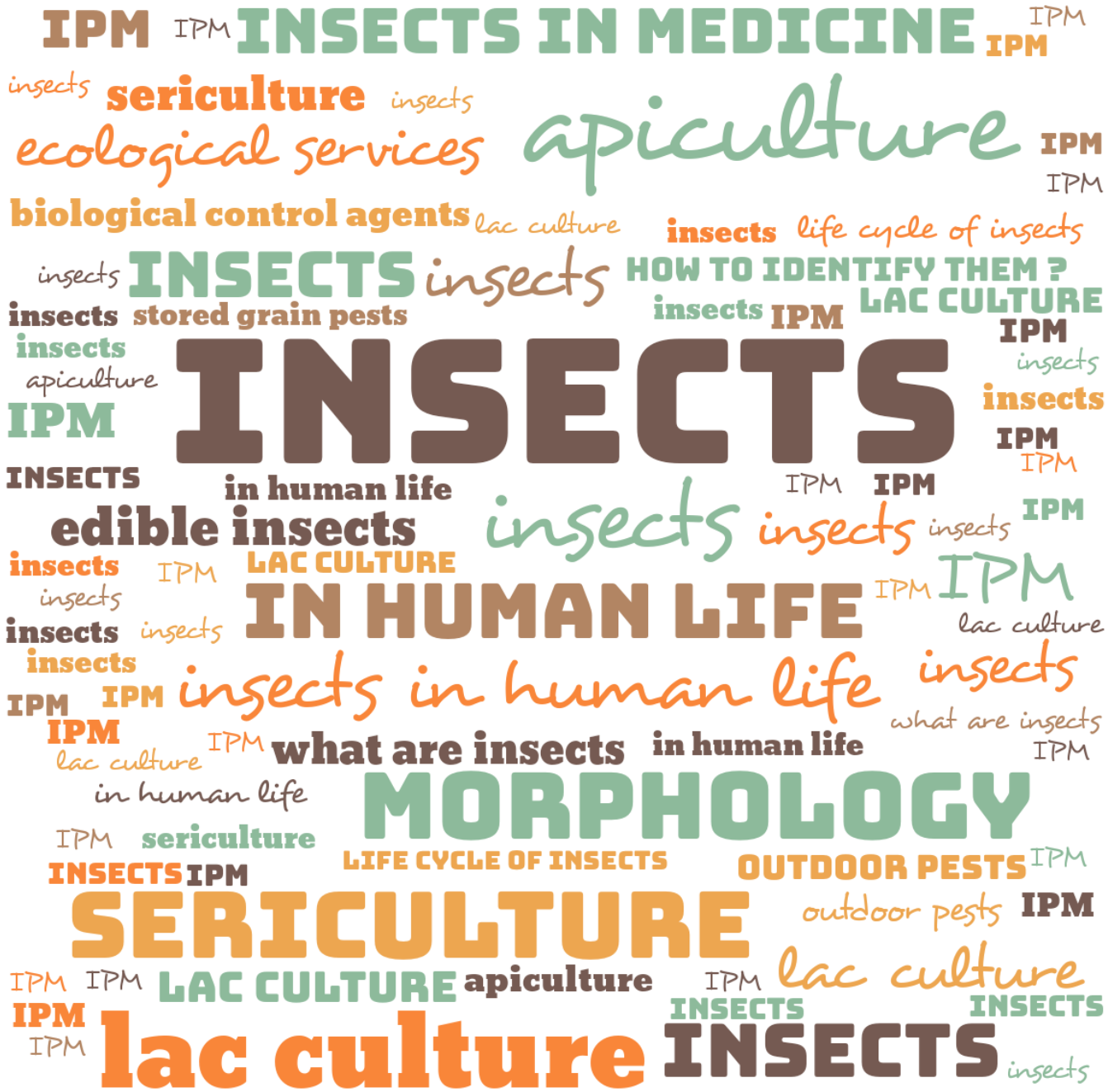

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Insect

Insects or **Insecta** (from Latin *insectum*) are hexapod invertebrates and the largest group within the arthropod phylum. Definitions and circumscriptions vary; usually, insects comprise a class within the Arthropoda. As used here, the term Insecta is synonymous with **Ectognatha**. Insects have a chitinous exoskeleton, a three-part body (head, thorax and abdomen), three pairs of jointed legs, compound eyes and one pair of antennae. Insects are the most diverse group of animals; they include more than a million described species and represent more than half of all known living organisms.[2][3] The total number of extant species is estimated at between six and ten million;[2][4][5] potentially over 90% of the animal life forms on Earth are insects.[5][6] Insects may be found in nearly all environments, although only a small number of species reside in the oceans, which are dominated by another arthropod group, crustaceans.

Nearly all insects hatch from eggs. Insect growth is constrained by the inelastic exoskeleton and development involves a series of molts. The immature stages often differ from the adults in structure, habit and habitat, and can include a passive pupal stage in those groups that undergo four-stage metamorphosis. Insects that undergo three-stage metamorphosis lack a pupal stage and adults develop through a series of nymphal stages.[7] The higher level relationship of the insects is unclear. Fossilized insects of enormous size have been found from the Paleozoic Era, including giant dragonflies with wingspans of 55 to 70 cm (22 to 28 in). The most diverse insect groups appear to have coevolved with flowering plants.

Adult insects typically move about by walking, flying, or sometimes swimming. As it allows for rapid yet stable movement, many insects adopt a tripedal gait in which they walk with their legs touching the ground in alternating triangles, composed of the front & rear on one side with the middle on the other side. Insects are the only invertebrates to have evolved flight, and all flying insects derive from one common ancestor. Many insects spend at least part of their lives under water, with larval adaptations that include gills, and some adult insects are aquatic and have adaptations for swimming. Some species, such as water striders, are capable of walking on the surface of water. Insects are mostly solitary, but some, such as certain bees, ants and termites, are social and live in large, well-organized colonies. Some insects, such as earwigs, show maternal care, guarding their eggs and young. Insects can communicate with each other in a variety of ways. Male moths can sense the pheromones of female moths over great distances. Other species communicate with sounds: crickets stridulate, or rub their wings together, to attract a mate and repel other males. Lampyrid beetles communicate with light.

Insect

Temporal range: 396–0 Ma

Pre	Є	O	S	D	C	P	T	J	K	Pg	N

Early Devonian[1] **(but see text) – Present**



Clockwise from top left: dance fly (*Empis livida*), long-nosed weevil (*Rhinotia hemistictus*), mole cricket (*Gryllotalpa brachyptera*), German wasp (*Vespula germanica*), emperor gum moth (*Opodiphthera eucalypti*), assassin bug (Harpactorinae)

0:00 / 0:00

A chorus of several *Magicicada* species

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Clade:	Pancrustacea
Subphylum:	Hexapoda
Class:	Insecta Linnaeus, 1758

Subgroups

See text.

Humans regard certain insects as pests, and attempt to control them using insecticides, and a host of other techniques. Some insects damage crops by feeding on sap, leaves, fruits, or wood. Some species are parasitic, and may vector diseases. Some insects perform complex ecological roles; blow-flies, for example, help consume carrion but also spread diseases. Insect pollinators are essential to the life cycle of many flowering plant species on which most organisms, including humans, are at least partly dependent; without them, the terrestrial portion of the biosphere would be devastated.[8] Many insects are considered ecologically beneficial as predators and a few provide direct economic benefit. Silkworms produce silk and honey bees produce honey and both have been domesticated by humans. Insects are consumed as food in 80% of the world's nations, by people in roughly 3000 ethnic groups.[9][10] Human activities also have effects on insect biodiversity.

Synonyms

- Ectognatha
- Entomida

Contents

Etymology

Definitions

Phylogeny and evolution
- Evolutionary relationships
- Taxonomy

Diversity

Morphology and physiology
- External
- Segmentation
 - Exoskeleton
- Internal
 - Nervous system
 - Digestive system
 - Foregut
 - Midgut
 - Hindgut
 - Excretory system
 - Reproductive system
 - Respiratory system
 - Circulatory system

Reproduction and development
- Metamorphosis
 - Incomplete metamorphosis
 - Complete metamorphosis

Senses and communication
- Light production and vision
- Sound production and hearing
- Chemical communication

Social behavior
- Care of young

Locomotion
- Flight
- Walking
 - Use in robotics

Swimming

Ecology
Defense and predation
Pollination
Parasitism

Relationship to humans
As pests
In beneficial roles
In research
As food
As pets
In culture

See also

References

Bibliography

Further reading

External links

Etymology

The word "insect" comes from the Latin word *insectum*, meaning "with a notched or divided body", or literally "cut into", from the neuter singular perfect passive participle of *insectare*, "to cut into, to cut up", from *in-* "into" and *secare* "to cut";[11] because insects appear "cut into" three sections. A calque of Greek ἔντομον [*éntomon*], "cut into sections", Pliny the Elder introduced the Latin designation as a loan-translation of the Greek word ἔντομος (*éntomos*) or "insect" (as in entomology), which was Aristotle's term for this class of life, also in reference to their "notched" bodies. "Insect" first appears documented in English in 1601 in Holland's translation of Pliny. Translations of Aristotle's term also form the usual word for "insect" in Welsh (*trychfil*, from *trychu* "to cut" and *mil*, "animal"), Serbo-Croatian (*zareznik*, from *rezati*, "to cut"), Russian (насекомое *nasekomoje*, from *seč'/-sekat'*, "to cut"), etc.[11][12]

Definitions

The precise definition of the taxon Insecta and the equivalent English name "insect" varies; three alternative definitions are shown in the table.

Definition of Insecta

<table>
<tr><th>Group</th><th colspan="3">Alternative definitions</th></tr>
<tr><td>Collembola (springtails)</td><td rowspan="6">Insecta sensu lato
=Hexapoda</td><td rowspan="3">Entognatha
(paraphyletic)</td><td rowspan="5">Apterygota
(wingless hexapods)
(paraphyletic)</td></tr>
<tr><td>Protura (coneheads)</td></tr>
<tr><td>Diplura (two-pronged bristletails)</td></tr>
<tr><td>Archaeognatha (jumping bristletails)</td><td rowspan="3">Insecta sensu stricto
=Ectognatha</td></tr>
<tr><td>Zygentoma (silverfish)</td></tr>
<tr><td>Pterygota (winged insects)</td><td>Insecta sensu strictissimo</td></tr>
</table>

In the broadest circumscription, Insecta *sensu lato* consists of all hexapods.[13][14] Traditionally, insects defined in this way were divided into "Apterygota" (the first five groups in the table)—the wingless insects—and Pterygota—the winged insects.[15] However, modern phylogenetic studies have shown that "Apterygota" is not monophyletic,[16] and so does not form a good

taxon. A narrower circumscription restricts insects to those hexapods with external mouthparts, and comprises only the last three groups in the table. In this sense, Insecta *sensu stricto* is equivalent to Ectognatha.[13][16] In the narrowest circumscription, insects are restricted to hexapods that are either winged or descended from winged ancestors. Insecta *sensu strictissimo* is then equivalent to Pterygota.[17] For the purposes of this article, the middle definition is used; insects consist of two wingless taxa, Archaeognatha (jumping bristletails) and Zygentoma (silverfish), plus the winged or secondarily wingless Pterygota.

Phylogeny and evolution

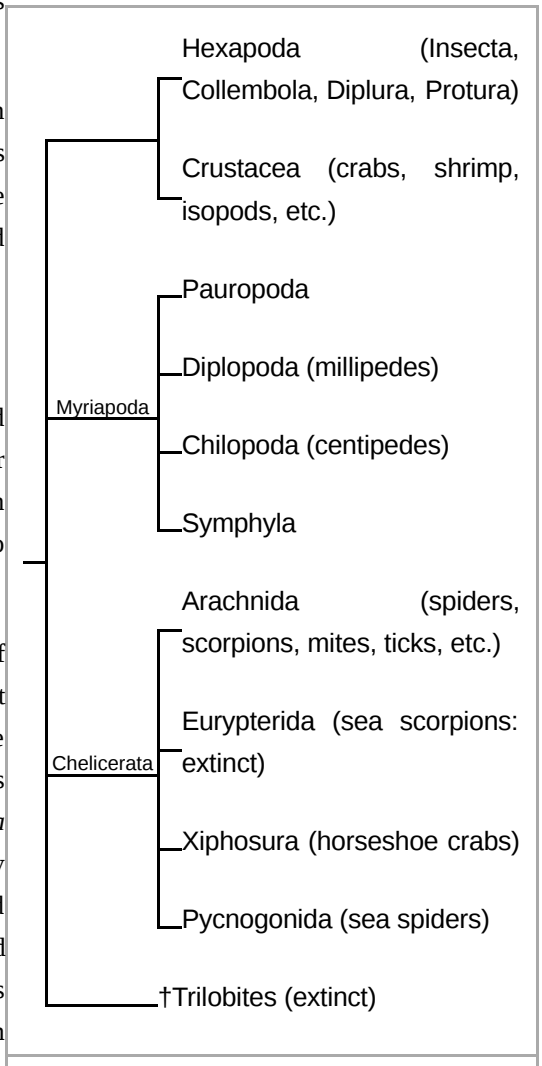
The evolutionary relationship of insects to other animal groups remains unclear.

Although traditionally grouped with millipedes and centipedes—possibly on the basis of convergent adaptations to terrestrialisation[19]—evidence has emerged favoring closer evolutionary ties with crustaceans. In the Pancrustacea theory, insects, together with Entognatha, Remipedia, and Cephalocarida, make up a natural clade labeled Miracrustacea.[20]

Insects form a single clade, closely related to crustaceans and myriapods.[21]

Other terrestrial arthropods, such as centipedes, millipedes, scorpions, and spiders, are sometimes confused with insects since their body plans can appear similar, sharing (as do all arthropods) a jointed exoskeleton. However, upon closer examination, their features differ significantly; most noticeably, they do not have the six-legged characteristic of adult insects.[22]

The higher-level phylogeny of the arthropods continues to be a matter of debate and research. In 2008, researchers at Tufts University uncovered what they believe is the world's oldest known full-body impression of a primitive flying insect, a 300-million-year-old specimen from the Carboniferous period.[23] The oldest definitive insect fossil is the Devonian *Rhyniognatha hirsti*, from the 396-million-year-old Rhynie chert. It may have superficially resembled a modern-day silverfish insect. This species already possessed dicondylic mandibles (two articulations in the mandible), a feature associated with winged insects, suggesting that wings may already have evolved at this time. Thus, the first insects probably appeared earlier, in the Silurian period.[1][24]



A phylogenetic tree of the arthropods and related groups[18]

Four super radiations of insects have occurred: beetles (evolved about 300 million years ago), flies (evolved about 250 million years ago), and moths and wasps (evolved about 150 million years ago).[25] These four groups account for the majority of described species. The flies and moths along with the fleas evolved from the Mecoptera.

The origins of insect flight remain obscure, since the earliest winged insects currently known appear to have been capable fliers. Some extinct insects had an additional pair of winglets attaching to the first segment of the thorax, for a total of three pairs. As of 2009, no evidence suggests the insects were a particularly successful group of animals before they evolved to have wings.[26]

Late Carboniferous and Early Permian insect orders include both extant groups, their stem groups,[27] and a number of Paleozoic groups, now extinct. During this era, some giant dragonfly-like forms reached wingspans of 55 to 70 cm (22 to 28 in), making them far larger than any living insect. This gigantism may have been due to higher atmospheric oxygen levels that allowed increased respiratory efficiency relative to today. The lack of flying vertebrates could have been another factor. Most extinct

orders of insects developed during the Permian period that began around 270 million years ago. Many of the early groups became extinct during the Permian-Triassic extinction event, the largest mass extinction in the history of the Earth, around 252 million years ago.[28]

The remarkably successful Hymenoptera appeared as long as 146 million years ago in the Cretaceous period, but achieved their wide diversity more recently in the Cenozoic era, which began 66 million years ago. A number of highly successful insect groups evolved in conjunction with flowering plants, a powerful illustration of coevolution.[29]

Many modern insect genera developed during the Cenozoic. Insects from this period on are often found preserved in amber, often in perfect condition. The body plan, or morphology, of such specimens is thus easily compared with modern species. The study of fossilized insects is called paleoentomology.



Evolution has produced enormous variety in insects. Pictured are some possible shapes of antennae.

Evolutionary relationships

Insects are prey for a variety of organisms, including terrestrial vertebrates. The earliest vertebrates on land existed 400 million years ago and were large amphibious piscivores. Through gradual evolutionary change, insectivory was the next diet type to evolve.[30]

Insects were among the earliest terrestrial herbivores and acted as major selection agents on plants.[29] Plants evolved chemical defenses against this herbivory and the insects, in turn, evolved mechanisms to deal with plant toxins. Many insects make use of these toxins to protect themselves from their predators. Such insects often advertise their toxicity using warning colors.[31] This successful evolutionary pattern has also been used by mimics. Over time, this has led to complex groups of coevolved species. Conversely, some interactions between plants and insects, like pollination, are beneficial to both organisms. Coevolution has led to the development of very specific mutualisms in such systems.

Taxonomy

Traditional morphology-based or appearance-based systematics have usually given the Hexapoda the rank of superclass,[33]:180 and identified four groups within it: insects (Ectognatha), springtails (Collembola), Protura, and Diplura, the latter three being grouped together as the Entognatha on the basis of internalized mouth parts. Supraordinal relationships have undergone numerous changes with the advent of methods based on evolutionary history and genetic data. A recent theory is that the Hexapoda are polyphyletic (where the last common ancestor was not a member of the group), with the entognath classes having separate evolutionary histories from the Insecta.[34] Many of the traditional appearance-based taxa have been shown to be paraphyletic, so rather than using ranks like subclass, superorder, and infraorder, it has proved better to use monophyletic groupings (in which the last common ancestor is a member of the group). The following represents the best-supported monophyletic groupings for the Insecta.

Insects can be divided into two groups historically treated as subclasses: wingless insects, known as Apterygota, and winged insects, known as Pterygota. The Apterygota consist of the primitively wingless order of the silverfish (Zygentoma). Archaeognatha make up the Monocondylia based on the shape of their mandibles, while Zygentoma and Pterygota are grouped together as Dicondylia. The Zygentoma themselves possibly are not monophyletic, with the family Lepidotrichidae being a sister group to the Dicondylia (Pterygota and the remaining Zygentoma).[35][36]

Paleoptera and Neoptera are the winged orders of insects differentiated by the presence of hardened body parts called sclerites, and in the Neoptera, muscles that allow their wings to fold flatly over the abdomen. Neoptera can further be divided into incomplete metamorphosis-based (Polyneoptera and Paraneoptera) and complete metamorphosis-based groups. It has proved difficult to clarify the relationships between the orders in Polyneoptera because of constant new findings calling for revision of the taxa. For example, the Paraneoptera have turned out to be more closely related to the Endopterygota than to the rest of the Exopterygota. The recent molecular finding that the traditional louse orders Mallophaga and Anoplura are derived from within Psocoptera has led to the new taxon Psocodea.[37] Phasmatodea and Embiidina have been suggested to form the Eukinolabia.[38] Mantodea, Blattodea, and Isoptera are thought to form a monophyletic group termed Dictyoptera.[39]

The Exopterygota likely are paraphyletic in regard to the Endopterygota. Matters that have incurred controversy include Strepsiptera and Diptera grouped together as Halteria based on a reduction of one of the wing pairs—a position not well-supported in the entomological community.[40] The Neuropterida are often lumped or split on the whims of the taxonomist. Fleas are now thought to be closely related to boreid mecopterans.[41] Many questions remain in the basal relationships among endopterygote orders, particularly the Hymenoptera.

The study of the classification or taxonomy of any insect is called systematic entomology. If one works with a more specific order or even a family, the term may also be made specific to that order or family, for example systematic dipterology.

Classification

Insecta

Monocondylia

-Archaeognatha - 470

Dicondylia

Apterygota

-Zygentoma<200

-Monura

Pterygota

Paleoptera

-Ephemeroptera-2,500–<3,000

-Odonata- 6,500

Neoptera

-Blattodea – 3,684–4,000

-Coleoptera – 360,000–400,000

-Dermaptera – 1,816

-Diptera – 152,956

-Embioptera – 200–300

-Hemiptera – 50,000–80,000

-Hymenoptera – 115,000

-Lepidoptera – 174,250

-Mantodea – 2,200

-Mecoptera – 481

-Megaloptera – 250–300

-Neuroptera – 5,000

-Notoptera – 30

-Orthoptera – 24,380

-Phasmatodea – 2,500–3,300

-Phthiraptera – 3,000–3,200

-Plecoptera – 2,274

-Psocoptera – 5,500

-Raphidioptera – 210

-Siphonaptera – 2,525

-Strepsiptera – 596

-Thysanoptera – 5,000

-Trichoptera –

Diversity

Estimates on the total number of insect species, or those within specific orders, often vary considerably. Globally, averages of these estimates suggest there are around 1.5 million beetle species and 5.5 million insect species, with about 1 million insect species currently found and described.[42]

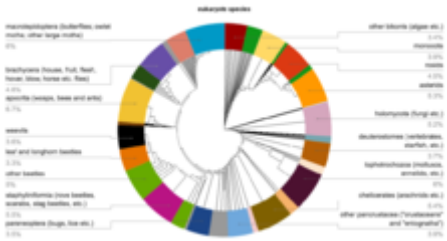
Between 950,000–1,000,000 of all described species are insects, so over 50% of all described eukaryotes (1.8 million) are insects (see illustration). With only 950,000 known non-insects, if the actual number of insects is 5.5 million, they may represent over 80% of the total. As only about 20,000 new species of all organisms are described each year, most insect species may remain undescribed, unless the rate of species descriptions greatly increases. Of the 24

orders of insects, four dominate in terms of numbers of described species; at least 670,000 identified species belong to Coleoptera, Diptera, Hymenoptera or Lepidoptera.

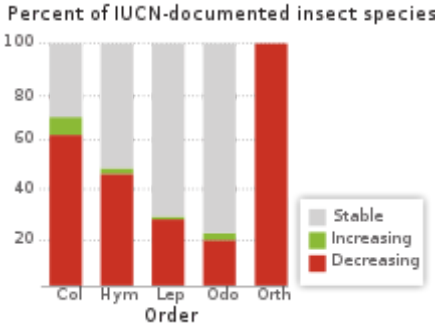
As of 2017, at least 66 insect species extinctions had been recorded in the previous 500 years, which generally occurred on oceanic islands.[44] Declines in insect abundance have been attributed to artificial lighting,[45] land use changes such as urbanization or agricultural use,[46][47] pesticide use,[48] and invasive species.[49] Studies summarized in a 2019 review suggested a large proportion of insect species are threatened with extinction in the 21st century.[50] Though ecologist Manu Sanders notes the 2019 review was biased by mostly excluding data showing increases or stability in insect population, with the studies limited to specific geographic areas and specific groups of species.[51] Claims of pending mass insect extinctions or "insect apocalypse" based on a subset of these studies have been popularized in news reports, but often extrapolate beyond the study data or hyperbolize study findings.[52] For some insect groups such as some butterflies, bees, and beetles, declines in abundance and diversity have been documented in European studies. Other areas have shown increases in some insect species, although trends in most regions are currently unknown. It is difficult to assess long-term trends in insect abundance or diversity because historical measurements are generally not known for many species. Robust data to assess at-risk areas or species is especially lacking for arctic and tropical regions and a majority of the southern hemisphere.[52]

12,627
-Zoraptera – 28

Cladogram of living insect groups,[32] with numbers of species in each group.[5] The Apterygota, Palaeoptera, and Exopterygota are possibly paraphyletic groups.



A pie chart of described eukaryote species, showing just over half of these to be insects



Insects with population trends documented by the International Union for Conservation of Nature, for orders *Collembola, Hymenoptera, Lepidoptera, Odonata,* and *Orthoptera.* Of 203 insect species that had such documented population trends in 2013, 33% were in decline.[43]

Estimates of total extant insect species[42]

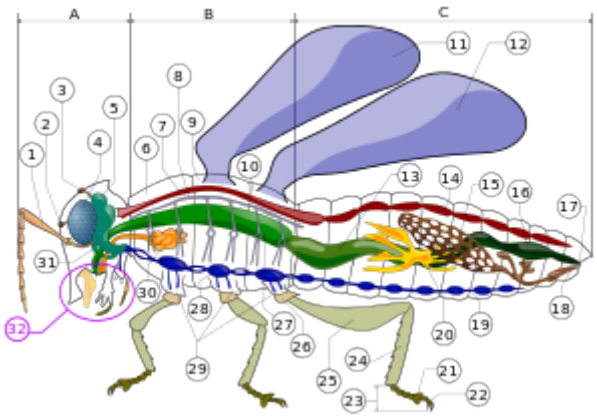
Order	Estimated total species
Archaeognatha	513
Zygentoma	560
Ephemeroptera	3,240
Odonata	5,899
Orthoptera	23,855
Neuroptera	5,868
Phasmida	3,014
Embioptera	463
Grylloblattodea	34
Mantophasmatodea	20
Plecoptera	3,743
Dermaptera	1,978
Zoraptera	37
Mantodea	2,400
Blattodea	7,314
Psocoptera	5,720
Phthiraptera	5,102
Thysanoptera	5,864
Hemiptera	103,590
Hymenoptera	116,861
Strepsiptera	609
Coleoptera	386,500
Megaloptera	354
Raphidioptera	254
Trichoptera	14,391
Lepidoptera	157,338
Diptera	155,477
Siphonaptera	2,075
Mecoptera	757

Morphology and physiology

External

Insects have segmented bodies supported by exoskeletons, the hard outer covering made mostly of chitin. The segments of the body are organized into three distinctive but interconnected units, or tagmata: a head, a thorax and an abdomen.[53] The head supports a pair of sensory antennae, a pair of compound eyes, zero to three simple eyes (or ocelli) and three sets of variously

modified appendages that form the mouthparts. The thorax is made up of three segments: the prothorax, mesothorax and the metathorax. Each thoracic segment supports one pair of legs. The meso- and metathoracic segments may each have a pair of wings, depending on the insect. The abdomen consists of eleven segments, though in a few species of insects, these segments may be fused together or reduced in size. The abdomen also contains most of the digestive, respiratory, excretory and reproductive internal structures.[33]:22–48 Considerable variation and many adaptations in the body parts of insects occur, especially wings, legs, antenna and mouthparts.



Insect morphology
A- Head **B**- Thorax **C**- Abdomen

1. antenna
2. ocelli (lower)
3. ocelli (upper)
4. compound eye
5. brain (cerebral ganglia)
6. prothorax
7. dorsal blood vessel
8. tracheal tubes (trunk with spiracle)
9. mesothorax
10. metathorax
11. forewing
12. hindwing
13. mid-gut (stomach)
14. dorsal tube (Heart)
15. ovary
16. hind-gut (intestine, rectum & anus)
17. anus
18. oviduct
19. nerve chord (abdominal ganglia)
20. Malpighian tubes
21. tarsal pads
22. claws
23. tarsus
24. tibia
25. femur
26. trochanter
27. fore-gut (crop, gizzard)
28. thoracic ganglion
29. coxa
30. salivary gland
31. subesophageal ganglion
32. mouthparts

Segmentation

The head is enclosed in a hard, heavily sclerotized, unsegmented, exoskeletal head capsule, or epicranium, which contains most of the sensing organs, including the antennae, ocellus or eyes, and the mouthparts. Of all the insect orders, Orthoptera displays the most features found in other insects, including the sutures and sclerites.[54] Here, the vertex, or the apex (dorsal region), is situated between the compound eyes for insects with a hypognathous and opisthognathous head. In prognathous insects, the vertex is not found between the compound eyes, but rather, where the ocelli are normally. This is because the primary axis of the head is rotated 90° to become parallel to the primary axis of the body. In some species, this region is modified and assumes a different name.[54]:13

The thorax is a tagma composed of three sections, the prothorax, mesothorax and the metathorax. The anterior segment, closest to the head, is the prothorax, with the major features being the first pair of legs and the pronotum. The middle segment is the mesothorax, with the major features being the second pair of legs and the anterior wings. The third and most posterior segment, abutting the abdomen, is the metathorax, which features the third pair of legs and the posterior wings. Each segment is dilineated by an intersegmental suture. Each segment has four basic regions. The dorsal surface is called the tergum (or *notum*) to distinguish it from the abdominal terga.[33] The two lateral regions are called the pleura (singular: pleuron) and the ventral aspect is called the sternum. In turn, the notum of the prothorax is called the pronotum, the notum for the mesothorax is called the mesonotum and the notum for the metathorax is called the metanotum. Continuing with this logic, the mesopleura and metapleura, as well as the mesosternum and metasternum, are used.[54]

The abdomen is the largest tagma of the insect, which typically consists of 11–12 segments and is less strongly sclerotized than the head or thorax. Each segment of the abdomen is represented by a sclerotized tergum and sternum. Terga are separated from each other and from the adjacent sterna or pleura by membranes. Spiracles are located in the pleural area. Variation of this ground plan includes the fusion of terga or terga and sterna to form continuous dorsal or ventral shields or a conical tube. Some insects bear a sclerite in the pleural area called a laterotergite. Ventral sclerites are sometimes called laterosternites. During the embryonic stage of many insects and the postembryonic stage of primitive insects, 11 abdominal segments are present. In modern insects there is a tendency toward reduction in the number of the abdominal segments, but the primitive number of 11 is

maintained during embryogenesis. Variation in abdominal segment number is considerable. If the Apterygota are considered to be indicative of the ground plan for pterygotes, confusion reigns: adult Protura have 12 segments, Collembola have 6. The orthopteran family Acrididae has 11 segments, and a fossil specimen of Zoraptera has a 10-segmented abdomen.[54]

Exoskeleton

The insect outer skeleton, the cuticle, is made up of two layers: the epicuticle, which is a thin and waxy water resistant outer layer and contains no chitin, and a lower layer called the procuticle. The procuticle is chitinous and much thicker than the epicuticle and has two layers: an outer layer known as the exocuticle and an inner layer known as the endocuticle. The tough and flexible endocuticle is built from numerous layers of fibrous chitin and proteins, criss-crossing each other in a sandwich pattern, while the exocuticle is rigid and hardened.[33]:22–24 The exocuticle is greatly reduced in many insects during their larval stages, e.g., caterpillars. It is also reduced in soft-bodied adult insects.

Insects are the only invertebrates to have developed active flight capability, and this has played an important role in their success.[33]:186 Their flight muscles are able to contract multiple times for each single nerve impulse, allowing the wings to beat faster than would ordinarily be possible.

Having their muscles attached to their exoskeletons is efficient and allows more muscle connections.

Internal

Nervous system

The nervous system of an insect can be divided into a brain and a ventral nerve cord. The head capsule is made up of six fused segments, each with either a pair of ganglia, or a cluster of nerve cells outside of the brain. The first three pairs of ganglia are fused into the brain, while the three following pairs are fused into a structure of three pairs of ganglia under the insect's esophagus, called the subesophageal ganglion.[33]:57

The thoracic segments have one ganglion on each side, which are connected into a pair, one pair per segment. This arrangement is also seen in the abdomen but only in the first eight segments. Many species of insects have reduced numbers of ganglia due to fusion or reduction.[55] Some cockroaches have just six ganglia in the abdomen, whereas the wasp *Vespa crabro* has only two in the thorax and three in the abdomen. Some insects, like the house fly *Musca domestica*, have all the body ganglia fused into a single large thoracic ganglion.

At least a few insects have nociceptors, cells that detect and transmit signals responsible for the sensation of pain.[56] This was discovered in 2003 by studying the variation in reactions of larvae of the common fruitfly Drosophila to the touch of a heated probe and an unheated one. The larvae reacted to the touch of the heated probe with a stereotypical rolling behavior that was not exhibited when the larvae were touched by the unheated probe.[57] Although nociception has been demonstrated in insects, there is no consensus that insects feel pain consciously[58]

Insects are capable of learning.[59]

Digestive system

An insect uses its digestive system to extract nutrients and other substances from the food it consumes.[60] Most of this food is ingested in the form of macromolecules and other complex substances like proteins, polysaccharides, fats and nucleic acids. These macromolecules must be broken down by catabolic reactions into smaller molecules like amino acids and simple sugars before being used by cells of the body for energy, growth, or reproduction. This break-down process is known as digestion.

It should be emphasized that there is extensive variation among different orders, life stages, and even castes in the digestive system of insects.[61] This is the result of extreme adaptations to various lifestyles. The present description focus on a generalized composition of the digestive system of an adult orthopteroid insect, which is considered basal to interpreting particularities of other groups.

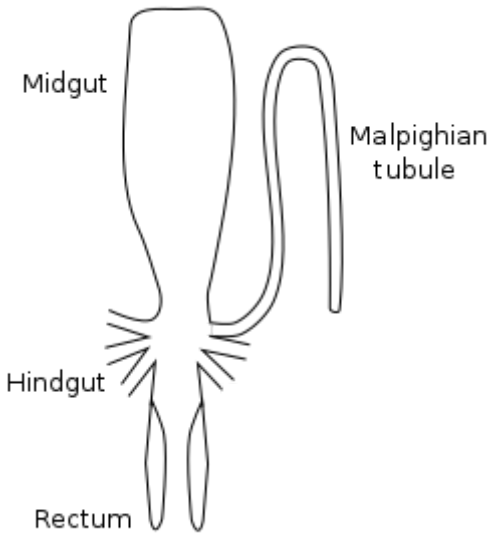
The main structure of an insect's digestive system is a long enclosed tube called the alimentary canal, which runs lengthwise through the body. The alimentary canal directs food unidirectionally from the mouth to the anus. It has three sections, each of which performs a different process of digestion. In addition to the alimentary canal, insects also have paired salivary glands and salivary reservoirs. These structures usually reside in the thorax, adjacent to the foregut.[33]:70–77 The salivary glands (element 30 in numbered diagram) in an insect's mouth produce saliva. The salivary ducts lead from the glands to the reservoirs and then forward through the head to an opening called the salivarium, located behind the hypopharynx. By moving its mouthparts (element 32 in numbered diagram) the insect can mix its food with saliva. The mixture of saliva and food then travels through the salivary tubes into the mouth, where it begins to break down.[62][63] Some insects, like flies, have extra-oral digestion. Insects using extra-oral digestion expel digestive enzymes onto their food to break it down. This strategy allows insects to extract a significant proportion of the available nutrients from the food source.[64]:31 The gut is where almost all of insects' digestion takes place. It can be divided into the foregut, midgut and hindgut.

Foregut

The first section of the alimentary canal is the foregut (element 27 in numbered diagram), or stomodaeum. The foregut is lined with a cuticular lining made of chitin and proteins as protection from tough food. The foregut includes the buccal cavity (mouth), pharynx, esophagus and crop and proventriculus (any part may be highly modified), which both store food and signify when to continue passing onward to the midgut.[33]:70

Digestion starts in buccal cavity (mouth) as partially chewed food is broken down by saliva from the salivary glands. As the salivary glands produce fluid and carbohydrate-digesting enzymes (mostly amylases), strong muscles in the pharynx pump fluid into the buccal cavity, lubricating the food like the salivarium does, and helping blood feeders, and xylem and phloem feeders.

From there, the pharynx passes food to the esophagus, which could be just a simple tube passing it on to the crop and proventriculus, and then onward to the midgut, as in most insects. Alternately, the foregut may expand into a very enlarged crop and proventriculus, or the crop could just be a diverticulum, or fluid-filled structure, as in some Diptera species.[64]:30–31



Stylized diagram of insect digestive tract showing malpighian tubule, from an insect of the order Orthoptera

Midgut

Once food leaves the crop, it passes to the midgut (element 13 in numbered diagram), also known as the mesenteron, where the majority of digestion takes place. Microscopic projections from the midgut wall, called microvilli, increase the surface area of the wall and allow more nutrients to be absorbed; they tend to be close to the origin of the midgut. In some insects, the role of the microvilli and where they are located may vary. For example, specialized microvilli producing digestive enzymes may more likely be near the end of the midgut, and absorption near the origin or beginning of the midgut.[64]:32

Hindgut



Bumblebee defecating. Note the contraction of the abdomen to provide internal pressure

In the hindgut (element 16 in numbered diagram), or proctodaeum, undigested food particles are joined by uric acid to form fecal pellets. The rectum absorbs 90% of the water in these fecal pellets, and the dry pellet is then eliminated through the anus (element 17), completing the process of digestion. Envaginations at the anterior end of the hindgut form the Malpighian tubules, which form the main excretory system of insects.

Excretory system

Insects may have one to hundreds of Malpighian tubules (element 20). These tubules remove nitrogenous wastes from the hemolymph of the insect and regulate osmotic balance. Wastes and solutes are emptied directly into the alimentary canal, at the junction between the midgut and hindgut.[33]:71–72, 78–80

Reproductive system

The reproductive system of female insects consist of a pair of ovaries, accessory glands, one or more spermathecae, and ducts connecting these parts. The ovaries are made up of a number of egg tubes, called ovarioles, which vary in size and number by species. The number of eggs that the insect is able to make vary by the number of ovarioles with the rate that eggs can develop being also influenced by ovariole design. Female insects are able make eggs, receive and store sperm, manipulate sperm from different males, and lay eggs. Accessory glands or glandular parts of the oviducts produce a variety of substances for sperm maintenance, transport and fertilization, as well as for protection of eggs. They can produce glue and protective substances for coating eggs or tough coverings for a batch of eggs called oothecae. Spermathecae are tubes or sacs in which sperm can be stored between the time of mating and the time an egg is fertilized.[54]:880

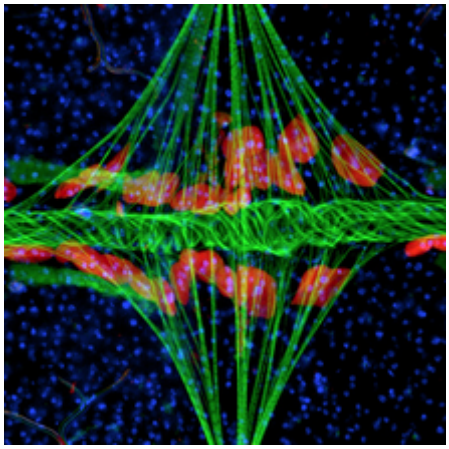
For males, the reproductive system is the testis, suspended in the body cavity by tracheae and the fat body. Most male insects have a pair of testes, inside of which are sperm tubes or follicles that are enclosed within a membranous sac. The follicles connect to the vas deferens by the vas efferens, and the two tubular vasa deferentia connect to a median ejaculatory duct that leads to the outside. A portion of the vas deferens is often enlarged to form the seminal vesicle, which stores the sperm before they are discharged into the female. The seminal vesicles have glandular linings that secrete nutrients for nourishment and maintenance of the sperm. The ejaculatory duct is derived from an invagination of the epidermal cells during development and, as a result, has a cuticular lining. The terminal portion of the ejaculatory duct may be sclerotized to form the intromittent organ, the aedeagus. The remainder of the male reproductive system is derived from embryonic mesoderm, except for the germ cells, or spermatogonia, which descend from the primordial pole cells very early during embryogenesis.[54]:885

Respiratory system

Insect respiration is accomplished without lungs. Instead, the insect respiratory system uses a system of internal tubes and sacs through which gases either diffuse or are actively pumped, delivering oxygen directly to tissues that need it via their trachea (element 8 in numbered diagram). In most insects, air is taken in through openings on the sides of the abdomen and thorax called spiracles.

The respiratory system is an important factor that limits the size of insects. As insects get larger, this type of oxygen transport is less efficient and thus the heaviest insect currently weighs less than 100 g. However, with increased atmospheric oxygen levels, as were present in the late Paleozoic, larger insects were possible, such as dragonflies with wingspans of more than two feet.[65]

There are many different patterns of gas exchange demonstrated by different groups of insects. Gas exchange patterns in insects can range from continuous and diffusive ventilation, to discontinuous gas exchange.[33]:65–68 During continuous gas exchange, oxygen is taken in and carbon dioxide is released in a continuous cycle. In discontinuous gas exchange, however, the insect takes in oxygen while it is active and small amounts of carbon dioxide are released when the insect is at rest.[66] Diffusive ventilation is simply a form of continuous gas exchange that occurs by diffusion rather than physically taking in the oxygen. Some species of insect that are submerged also have adaptations to aid in respiration. As larvae, many insects have gills that can extract oxygen dissolved in water, while others need to rise to the water surface to replenish air supplies, which may be held or trapped in special structures.[67][68]



The tube-like heart (green) of the mosquito *Anopheles gambiae* extends horizontally across the body, interlinked with the diamond-shaped wing muscles (also green) and surrounded by pericardial cells (red). Blue depicts cell nuclei.

Circulatory system

Because oxygen is delivered directly to tissues via tracheoles, the circulatory system is not used to carry oxygen, and is therefore greatly reduced. The insect circulatory system is open; it has no veins or arteries, and instead consists of little more than a single, perforated dorsal tube that pulses peristaltically. This dorsal blood vessel (element 14) is divided into two sections: the heart and aorta. The dorsal blood vessel circulates the hemolymph, arthropods' fluid analog of blood, from the rear of the body cavity forward.[33]:61–65[69] Hemolymph is composed of plasma in which hemocytes are suspended. Nutrients, hormones, wastes, and other substances are transported throughout the insect body in the hemolymph. Hemocytes include many types of cells that are important for immune responses, wound healing, and other functions. Hemolymph pressure may be increased by muscle contractions or by swallowing air into the digestive system to aid in moulting.[70] Hemolymph is also a major part of the open circulatory system of other arthropods, such as spiders and crustaceans.[71][72]

Reproduction and development

The majority of insects hatch from eggs. The fertilization and development takes place inside the egg, enclosed by a shell (chorion) that consists of maternal tissue. In contrast to eggs of other arthropods, most insect eggs are drought resistant. This is because inside the chorion two additional membranes develop from embryonic tissue, the amnion and the serosa. This serosa secretes a cuticle rich in chitin that protects the embryo against desiccation. In Schizophora however the serosa does not develop, but these flies lay their eggs in damp places, such as rotting matter.[73] Some species of insects, like the cockroach *Blaptica dubia*, as well as juvenile aphids and tsetse flies, are ovoviviparous. The eggs of ovoviviparous animals develop entirely inside the female, and then hatch immediately upon being laid.[7] Some other species, such as those in the genus of cockroaches known as *Diploptera*, are viviparous, and thus gestate inside the mother and are born alive.[33]:129, 131, 134–135 Some insects, like parasitic wasps, show polyembryony, where a single fertilized egg divides into many and in some cases thousands of separate embryos.[33]:136–137 Insects may be *univoltine*, *bivoltine* or *multivoltine*, i.e. they may have one, two or many broods (generations) in a year.[74]

Other developmental and reproductive variations include haplodiploidy, polymorphism, paedomorphosis or peramorphosis, sexual dimorphism, parthenogenesis and more rarely hermaphroditism.[33]:143 In haplodiploidy, which is a type of sex-determination system, the offspring's sex is determined by the number of sets of chromosomes an individual receives. This system is typical in bees and wasps.[75] Polymorphism is where a species may have different *morphs* or *forms*, as in the oblong winged katydid, which has four different varieties: green, pink and yellow or tan. Some insects may retain phenotypes that are normally only seen in juveniles; this is called paedomorphosis. In peramorphosis, an opposite sort of phenomenon, insects take on previously unseen traits after they have matured into adults. Many insects display sexual dimorphism, in which males and



A pair of *Simosyrphus grandicornis* hoverflies mating in flight.



A pair of grasshoppers mating.

females have notably different appearances, such as the moth *Orgyia recens* as an exemplar of sexual dimorphism in insects.

Some insects use parthenogenesis, a process in which the female can reproduce and give birth without having the eggs fertilized by a male. Many aphids undergo a form of parthenogenesis, called cyclical parthenogenesis, in which they alternate between one or many generations of asexual and sexual reproduction.[76][77] In summer, aphids are generally female and parthenogenetic; in the autumn, males may be produced for sexual reproduction. Other insects produced by parthenogenesis are bees, wasps and ants, in which they spawn males. However, overall, most individuals are female, which are produced by fertilization. The males are haploid and the females are diploid.[7] More rarely, some insects display hermaphroditism, in which a given individual has both male and female reproductive organs.



The different forms of the male (top) and female (bottom) tussock moth *Orgyia recens* is an example of sexual dimorphism in insects.

Insect life-histories show adaptations to withstand cold and dry conditions. Some temperate region insects are capable of activity during winter, while some others migrate to a warmer climate or go into a state of torpor.[78] Still other insects have evolved mechanisms of diapause that allow eggs or pupae to survive these conditions.[79]

Metamorphosis

Metamorphosis in insects is the biological process of development all insects must undergo. There are two forms of metamorphosis: incomplete metamorphosis and complete metamorphosis.

Incomplete metamorphosis

Hemimetabolous insects, those with incomplete metamorphosis, change gradually by undergoing a series of molts. An insect molts when it outgrows its exoskeleton, which does not stretch and would otherwise restrict the insect's growth. The molting process begins as the insect's epidermis secretes a new epicuticle inside the old one. After this new epicuticle is secreted, the epidermis releases a mixture of enzymes that digests the endocuticle and thus detaches the old cuticle. When this stage is complete, the insect makes its body swell by taking in a large quantity of water or air, which makes the old cuticle split along predefined weaknesses where the old exocuticle was thinnest.[33]:142[80]

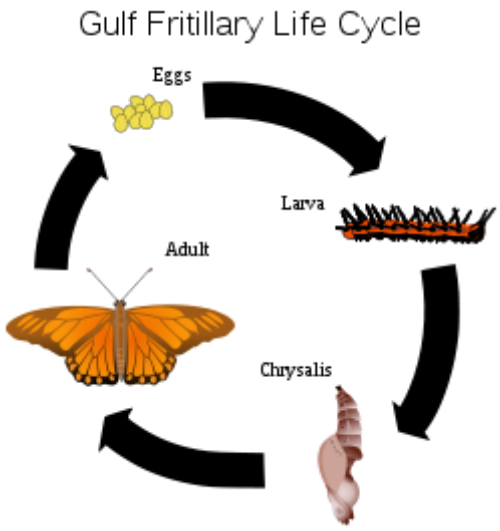
Immature insects that go through incomplete metamorphosis are called nymphs or in the case of dragonflies and damselflies, also naiads. Nymphs are similar in form to the adult except for the presence of wings, which are not developed until adulthood. With each molt, nymphs grow larger and become more similar in appearance to adult insects.



This southern hawker dragonfly molts its exoskeleton several times during its life as a nymph; shown is the final molt to become a winged adult (eclosion).

Complete metamorphosis

Holometabolism, or complete metamorphosis, is where the insect changes in four stages, an egg or embryo, a larva, a pupa and the adult or imago. In these species, an egg hatches to produce a larva, which is generally worm-like in form. This worm-like form can be one of several varieties: eruciform (caterpillar-like), scarabaeiform (grub-like), campodeiform (elongated, flattened and active), elateriform (wireworm-like) or vermiform (maggot-like). The larva grows and eventually becomes a pupa, a stage marked by reduced movement and often sealed within a cocoon. There are three types of pupae: obtect, exarate or coarctate. Obtect pupae are compact, with the legs and other appendages enclosed. Exarate pupae have their legs and other appendages free and extended. Coarctate pupae develop inside the larval skin.[33]:151 Insects undergo considerable change in form during the pupal stage, and emerge as adults. Butterflies are a well-known example of insects that undergo complete metamorphosis, although most insects use this life cycle. Some insects have evolved this system to hypermetamorphosis.



Gulf fritillary life cycle, an example of holometabolism.

Complete metamorphosis is a trait of the most diverse insect group, the Endopterygota.[33]:143 Endopterygota includes 11 Orders, the largest being Diptera (flies), Lepidoptera (butterflies and moths), and Hymenoptera (bees, wasps, and ants), and Coleoptera (beetles). This form of development is exclusive to insects and not seen in any other arthropods.

Senses and communication

Many insects possess very sensitive and specialized organs of perception. Some insects such as bees can perceive ultraviolet wavelengths, or detect polarized light, while the antennae of male moths can detect the pheromones of female moths over distances of many kilometers.[81] The yellow paper wasp (*Polistes versicolor*) is known for its wagging movements as a form of communication within the colony; it can waggle with a frequency of 10.6±2.1 Hz (n=190). These wagging movements can signal the arrival of new material into the nest and aggression between workers can be used to stimulate others to increase foraging expeditions.[82] There is a pronounced tendency for there to be a trade-off between visual acuity and chemical or tactile acuity, such that most insects with well-developed eyes have reduced or simple antennae, and vice versa. There are a variety of different mechanisms by which insects perceive sound; while the patterns are not universal, insects can generally hear sound if they can produce it. Different insect species can have varying hearing, though most insects can hear only a narrow range of frequencies

related to the frequency of the sounds they can produce. Mosquitoes have been found to hear up to 2 kHz, and some grasshoppers can hear up to 50 kHz.[83] Certain predatory and parasitic insects can detect the characteristic sounds made by their prey or hosts, respectively. For instance, some nocturnal moths can perceive the ultrasonic emissions of bats, which helps them avoid predation.[33]:87–94 Insects that feed on blood have special sensory structures that can detect infrared emissions, and use them to home in on their hosts.

Some insects display a rudimentary sense of numbers,[84] such as the solitary wasps that prey upon a single species. The mother wasp lays her eggs in individual cells and provides each egg with a number of live caterpillars on which the young feed when hatched. Some species of wasp always provide five, others twelve, and others as high as twenty-four caterpillars per cell. The number of caterpillars is different among species, but always the same for each sex of larva. The male solitary wasp in the genus *Eumenes* is smaller than the female, so the mother of one species supplies him with only five caterpillars; the larger female receives ten caterpillars in her cell.

Light production and vision

A few insects, such as members of the families Poduridae and Onychiuridae (Collembola), Mycetophilidae (Diptera) and the beetle families Lampyridae, Phengodidae, Elateridae and Staphylinidae are bioluminescent. The most familiar group are the fireflies, beetles of the family Lampyridae. Some species are able to control this light generation to produce flashes. The function varies with some species using them to attract mates, while others use them to lure prey. Cave dwelling larvae of *Arachnocampa* (Mycetophilidae, fungus gnats) glow to lure small flying insects into sticky strands of silk.[85] Some fireflies of the genus *Photuris* mimic the flashing of female *Photinus* species to attract males of that species, which are then captured and devoured.[86] The colors of emitted light vary from dull blue (*Orfelia fultoni*, Mycetophilidae) to the familiar greens and the rare reds (*Phrixothrix tiemanni*, Phengodidae).[87]


Most insects have compound eyes and two antennae.

Most insects, except some species of cave crickets, are able to perceive light and dark. Many species have acute vision capable of detecting minute movements. The eyes may include simple eyes or ocelli as well as compound eyes of varying sizes. Many species are able to detect light in the infrared, ultraviolet and the visible light wavelengths. Color vision has been demonstrated in many species and phylogenetic analysis suggests that UV-green-blue trichromacy existed from at least the Devonian period between 416 and 359 million years ago.[88]

Sound production and hearing

Insects were the earliest organisms to produce and sense sounds. Insects make sounds mostly by mechanical action of appendages. In grasshoppers and crickets, this is achieved by stridulation. Cicadas make the loudest sounds among the insects by producing and amplifying sounds with special modifications to their body to form tymbals and associated musculature. The African cicada *Brevisana brevis* has been measured at 106.7 decibels at a distance of 50 cm (20 in).[89] Some insects, such as the *Helicoverpa zea* moths, hawk moths and Hedylid butterflies, can hear ultrasound and take evasive action when they sense that they have been detected by bats.[90][91] Some moths produce ultrasonic clicks that were once thought to have a role in jamming bat echolocation. The ultrasonic clicks were subsequently found to be produced mostly by unpalatable moths to warn bats, just as warning colorations are used against predators that hunt by sight.[92] Some otherwise palatable moths have evolved to mimic

these calls.[93] More recently, the claim that some moths can jam bat sonar has been revisited. Ultrasonic recording and high-speed infrared videography of bat-moth interactions suggest the palatable tiger moth really does defend against attacking big brown bats using ultrasonic clicks that jam bat sonar.[94]

Very low sounds are also produced in various species of Coleoptera, Hymenoptera, Lepidoptera, Mantodea and Neuroptera. These low sounds are simply the sounds made by the insect's movement. Through microscopic stridulatory structures located on the insect's muscles and joints, the normal sounds of the insect moving are amplified and can be used to warn or communicate with other insects. Most sound-making insects also have tympanal organs that can perceive airborne sounds. Some species in Hemiptera, such as the corixids (water boatmen), are known to communicate via underwater sounds.[95] Most insects are also able to sense vibrations transmitted through surfaces.

Communication using surface-borne vibrational signals is more widespread among insects because of size constraints in producing air-borne sounds.[96] Insects cannot effectively produce low-frequency sounds, and high-frequency sounds tend to disperse more in a dense environment (such as foliage), so insects living in such environments communicate primarily using substrate-borne vibrations.[97] The mechanisms of production of vibrational signals are just as diverse as those for producing sound in insects.

0:00 / 0:00

Cricket in garage with familiar call.

Some species use vibrations for communicating within members of the same species, such as to attract mates as in the songs of the shield bug *Nezara viridula*.[98] Vibrations can also be used to communicate between entirely different species; lycaenid (gossamer-winged butterfly) caterpillars, which are myrmecophilous (living in a mutualistic association with ants) communicate with ants in this way.[99] The Madagascar hissing cockroach has the ability to press air through its spiracles to make a hissing noise as a sign of aggression;[100] the death's-head hawkmoth makes a squeaking noise by forcing air out of their pharynx when agitated, which may also reduce aggressive worker honey bee behavior when the two are in close proximity.[101]

Chemical communication

Chemical communications in animals rely on a variety of aspects including taste and smell. Chemoreception is the physiological response of a sense organ (i.e. taste or smell) to a chemical stimulus where the chemicals act as signals to regulate the state or activity of a cell. A semiochemical is a message-carrying chemical that is meant to attract, repel, and convey information. Types of semiochemicals include pheromones and kairomones. One example is the butterfly *Phengaris arion* which uses chemical signals as a form of mimicry to aid in predation.[102]

In addition to the use of sound for communication, a wide range of insects have evolved chemical means for communication. These chemicals, termed semiochemicals, are often derived from plant metabolites include those meant to attract, repel and provide other kinds of information. Pheromones, a type of semiochemical, are used for attracting mates of the opposite sex, for aggregating conspecific individuals of both sexes, for deterring other individuals from approaching, to mark a trail, and to trigger aggression in nearby individuals. Allomones benefit their producer by the effect they have upon the receiver. Kairomones benefit their receiver instead of their producer. Synomones benefit the producer and the receiver. While some chemicals are targeted at individuals of the same species, others are used for communication across species. The use of scents is especially well known to have developed in social insects.[33]:96–105

Social behavior

Social insects, such as termites, ants and many bees and wasps, are the most familiar species of eusocial animals.[103] They live together in large well-organized colonies that may be so tightly integrated and genetically similar that the colonies of some species are sometimes considered superorganisms. It is sometimes argued that the various species of honey bee are the only invertebrates (and indeed one of the few non-human groups) to have evolved a system of abstract symbolic communication where

a behavior is used to *represent* and convey specific information about something in the environment. In this communication system, called dance language, the angle at which a bee dances represents a direction relative to the sun, and the length of the dance represents the distance to be flown.[33]:309–311 Though perhaps not as advanced as honey bees, bumblebees also potentially have some social communication behaviors. *Bombus terrestris*, for example, exhibit a faster learning curve for visiting unfamiliar, yet rewarding flowers, when they can see a conspecific foraging on the same species.[104]

Only insects that live in nests or colonies demonstrate any true capacity for fine-scale spatial orientation or homing. This can allow an insect to return unerringly to a single hole a few millimeters in diameter among thousands of apparently identical holes clustered together, after a trip of up to several kilometers' distance. In a phenomenon known as philopatry, insects that hibernate have shown the ability to recall a specific location up to a year after last viewing the area of interest.[105] A few insects seasonally migrate large distances between different geographic regions (e.g., the overwintering areas of the monarch butterfly).[33]:14



A cathedral mound created by termites (Isoptera).

Care of young

The eusocial insects build nests, guard eggs, and provide food for offspring full-time (see Eusociality). Most insects, however, lead short lives as adults, and rarely interact with one another except to mate or compete for mates. A small number exhibit some form of parental care, where they will at least guard their eggs, and sometimes continue guarding their offspring until adulthood, and possibly even feeding them. Another simple form of parental care is to construct a nest (a burrow or an actual construction, either of which may be simple or complex), store provisions in it, and lay an egg upon those provisions. The adult does not contact the growing offspring, but it nonetheless does provide food. This sort of care is typical for most species of bees and various types of wasps.[106]

Locomotion

Flight

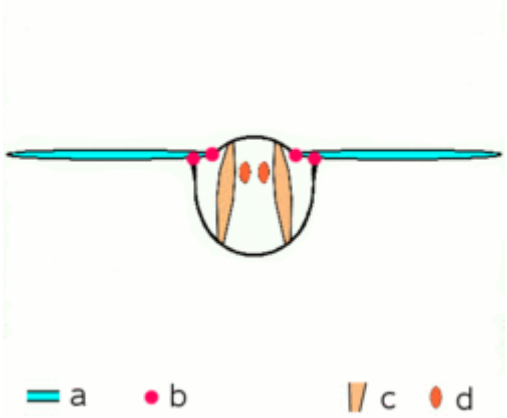
Insects are the only group of invertebrates to have developed flight. The evolution of insect wings has been a subject of debate. Some entomologists suggest that the wings are from paranotal lobes, or extensions from the insect's exoskeleton called the nota, called the *paranotal theory*. Other theories are based on a pleural origin. These theories include suggestions that wings originated from modified gills, spiracular flaps or as from an appendage of the epicoxa. The *epicoxal theory* suggests the insect wings are modified epicoxal exites, a modified appendage at the base of the legs or coxa.[107] In the Carboniferous age, some of the *Meganeura* dragonflies had as much as a 50 cm (20 in) wide wingspan. The appearance of gigantic insects has been found to be consistent with high atmospheric oxygen. The respiratory system of insects constrains their size, however the high oxygen in the atmosphere allowed larger sizes.[108] The largest flying insects today are much smaller and include several moth species such as the Atlas moth and the white witch (*Thysania agrippina*).



White-lined sphinx moth feeding in flight

Insect flight has been a topic of great interest in aerodynamics due partly to the inability of steady-state theories to explain the lift generated by the tiny wings of insects. But insect wings are in motion, with flapping and vibrations, resulting in churning and eddies, and the misconception that physics says "bumblebees can't fly" persisted throughout most of the twentieth century.

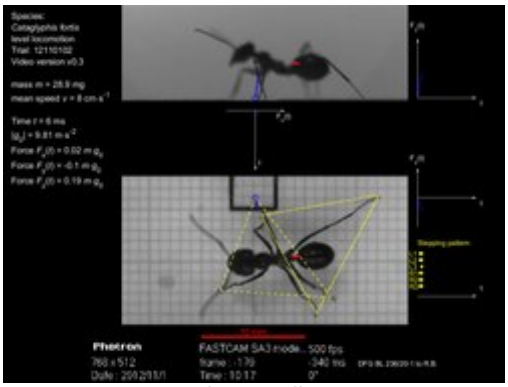
Unlike birds, many small insects are swept along by the prevailing winds[109] although many of the larger insects are known to make migrations. Aphids are known to be transported long distances by low-level jet streams.[110] As such, fine line patterns associated with converging winds within weather radar imagery, like the WSR-88D radar network, often represent large groups of insects.[111]



Basic motion of the insect wing in insect with an indirect flight mechanism scheme of dorsoventral cut through a thorax segment with
a wings
b joints
c dorsoventral muscles
d longitudinal muscles.

Walking

Many adult insects use six legs for walking and have adopted a tripedal gait. The tripedal gait allows for rapid walking while always having a stable stance and has been studied extensively in cockroaches and ants. The legs are used in alternate triangles touching the ground. For the first step, the middle right leg and the front and rear left legs are in contact with the ground and move the insect forward, while the front and rear right leg and the middle left leg are lifted and moved forward to a new position. When they touch the ground to form a new stable triangle the other legs can be lifted and brought forward in turn and so on.[112] The purest form of the tripedal gait is seen in insects moving at high speeds. However, this type of locomotion is not rigid and insects can adapt a variety of gaits. For example, when moving slowly, turning, avoiding obstacles, climbing or slippery surfaces, four (tetrapod) or more feet (wave-gait[113]) may be touching the ground. Insects can also adapt their gait to cope with the loss of one or more limbs.


Play media
Spatial and temporal stepping pattern of walking desert ants performing an alternating tripod gait. Recording rate: 500 fps, Playback rate: 10 fps.

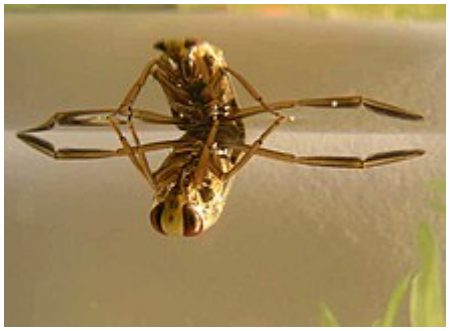
Cockroaches are among the fastest insect runners and, at full speed, adopt a bipedal run to reach a high velocity in proportion to their body size. As cockroaches move very quickly, they need to be video recorded at several hundred frames per second to reveal their gait. More sedate locomotion is seen in the stick insects or walking sticks (Phasmatodea). A few insects have evolved to walk on the surface of the water, especially members of the Gerridae family, commonly known as water striders. A few species of ocean-skaters in the genus *Halobates* even live on the surface of open oceans, a habitat that has few insect species.[114]

Use in robotics

Insect walking is of particular interest as an alternative form of locomotion in robots. The study of insects and bipeds has a significant impact on possible robotic methods of transport. This may allow new robots to be designed that can traverse terrain that robots with wheels may be unable to handle.[112]

Swimming

A large number of insects live either part or the whole of their lives underwater. In many of the more primitive orders of insect, the immature stages are spent in an aquatic environment. Some groups of insects, like certain water beetles, have aquatic adults as well.[67]



The backswimmer *Notonecta glauca* underwater, showing its paddle-like hindleg adaptation

Many of these species have adaptations to help in under-water locomotion. Water beetles and water bugs have legs adapted into paddle-like structures. Dragonfly naiads use jet propulsion, forcibly expelling water out of their rectal chamber.[115] Some species like the water striders are capable of walking on the surface of water. They can do this because their claws are not at the tips of the legs as in most insects, but recessed in a special groove further up the leg; this prevents the claws from piercing the water's surface film.[67] Other insects such as the Rove beetle *Stenus* are known to emit pygidial gland secretions that reduce surface tension making it possible for them to move on the surface of water by Marangoni propulsion (also known by the German term *Entspannungsschwimmen*).[116][117]

Ecology

Insect ecology is the scientific study of how insects, individually or as a community, interact with the surrounding environment or ecosystem.[118]:3 Insects play one of the most important roles in their ecosystems, which includes many roles, such as soil turning and aeration, dung burial, pest control, pollination and wildlife nutrition. An example is the beetles, which are scavengers that feed on dead animals and fallen trees and thereby recycle biological materials into forms found useful by other organisms.[119] These insects, and others, are responsible for much of the process by which topsoil is created.[33]:3, 218–228

Defense and predation

Insects are mostly soft bodied, fragile and almost defenseless compared to other, larger lifeforms. The immature stages are small, move slowly or are immobile, and so all stages are exposed to predation and parasitism. Insects then have a variety of defense strategies to avoid being attacked by predators or parasitoids. These include camouflage, mimicry, toxicity and active defense.[121]



Perhaps one of the most well-known examples of mimicry, the viceroy butterfly (top) appears very similar to the monarch butterfly (bottom).[120]

Camouflage is an important defense strategy, which involves the use of coloration or shape to blend into the surrounding environment.[122] This sort of protective coloration is common and widespread among beetle families, especially those that feed on wood or vegetation, such as many of the leaf beetles (family Chrysomelidae) or weevils. In some of these species, sculpturing or various colored scales or hairs cause the beetle to resemble bird dung or other inedible objects. Many of those that live in sandy environments blend in with the coloration of the substrate.[121] Most phasmids are known for effectively replicating the forms of sticks and leaves, and the bodies of some species (such as *O. macklotti* and *Palophus centaurus*) are covered in mossy or lichenous outgrowths that supplement their disguise. Very rarely, a species may have the ability to change color as their surroundings shift (*Bostra scabrinota*). In a further behavioral adaptation to supplement crypsis, a number of species have been noted to perform a rocking motion where the body is swayed from side to side that

is thought to reflect the movement of leaves or twigs swaying in the breeze. Another method by which stick insects avoid predation and resemble twigs is by feigning death (catalepsy), where the insect enters a motionless state that can be maintained for a long period. The nocturnal feeding habits of adults also aids Phasmatodea in remaining concealed from predators.[123]

Another defense that often uses color or shape to deceive potential enemies is mimicry. A number of longhorn beetles (family Cerambycidae) bear a striking resemblance to wasps, which helps them avoid predation even though the beetles are in fact harmless.[121] Batesian and Müllerian mimicry complexes are commonly found in Lepidoptera. Genetic polymorphism and natural selection give rise to otherwise edible species (the mimic) gaining a survival advantage by resembling inedible species (the model). Such a mimicry complex is referred to as *Batesian*. One of the most famous examples, where the viceroy butterfly was long believed to be a Batesian mimic of the inedible monarch, was later disproven, as the viceroy is more toxic than the monarch, and this resemblance is now considered to be a case of Müllerian mimicry.[120] In Müllerian mimicry, inedible species, usually within a taxonomic order, find it advantageous to resemble each other so as to reduce the sampling rate by predators who need to learn about the insects' inedibility. Taxa from the toxic genus *Heliconius* form one of the most well known Müllerian complexes.[124]

Chemical defense is another important defense found among species of Coleoptera and Lepidoptera, usually being advertised by bright colors, such as the monarch butterfly. They obtain their toxicity by sequestering the chemicals from the plants they eat into their own tissues. Some Lepidoptera manufacture their own toxins. Predators that eat poisonous butterflies and moths may become sick and vomit violently, learning not to eat those types of species; this is actually the basis of Müllerian mimicry. A predator who has previously eaten a poisonous lepidopteran may avoid other species with similar markings in the future, thus saving many other species as well.[125] Some ground beetles of the family Carabidae can spray chemicals from their abdomen with great accuracy, to repel predators.[121]

Pollination

Pollination is the process by which pollen is transferred in the reproduction of plants, thereby enabling fertilisation and sexual reproduction. Most flowering plants require an animal to do the transportation. While other animals are included as pollinators, the majority of pollination is done by insects.[126] Because insects usually receive benefit for the pollination in the form of energy rich nectar it is a grand example of mutualism. The various flower traits (and combinations thereof) that differentially attract one type of pollinator or another are known as pollination syndromes. These arose through complex plant-animal adaptations. Pollinators find flowers through bright colorations, including ultraviolet, and attractant pheromones. The study of pollination by insects is known as *anthecology*.



European honey bee carrying pollen in a pollen basket back to the hive

Parasitism

Many insects are parasites of other insects such as the parasitoid wasps. These insects are known as entomophagous parasites. They can be beneficial due to their devastation of pests that can destroy crops and other resources. Many insects have a parasitic relationship with humans such as the mosquito. These insects are known to spread diseases such as malaria and yellow fever and because of such, mosquitoes indirectly cause more deaths of humans than any other animal.

Relationship to humans

As pests

Many insects are considered pests by humans. Insects commonly regarded as pests include those that are parasitic (*e.g.* lice, bed bugs), transmit diseases (mosquitoes, flies), damage structures (termites), or destroy agricultural goods (locusts, weevils). Many entomologists are involved in various forms of pest control, as in research for companies to produce insecticides, but increasingly rely on methods of biological pest control, or biocontrol. Biocontrol uses one organism to reduce the population density of another organism—the pest—and is considered a key element of integrated pest management.[127][128]



Aedes aegypti, a parasite, is the vector of dengue fever and yellow fever

Despite the large amount of effort focused at controlling insects, human attempts to kill pests with insecticides can backfire. If used carelessly, the poison can kill all kinds of organisms in the area, including insects' natural predators, such as birds, mice and other insectivores. The effects of DDT's use exemplifies how some insecticides can threaten wildlife beyond intended populations of pest insects.[129][130]

In beneficial roles



Because they help flowering plants to cross-pollinate, some insects are critical to agriculture. This European honey bee is gathering nectar while pollen collects on its body.



A robberfly with its prey, a hoverfly. Insectivorous relationships such as these help control insect populations.

Although pest insects attract the most attention, many insects are beneficial to the environment and to humans. Some insects, like wasps, bees, butterflies and ants, pollinate flowering plants. Pollination is a mutualistic relationship between plants and insects. As insects gather nectar from different plants of the same species, they also spread pollen from plants on which they have previously fed. This greatly increases plants' ability to cross-pollinate, which maintains and possibly even improves their evolutionary fitness. This ultimately affects humans since ensuring healthy crops is critical to agriculture. As well as pollination ants help with seed distribution of plants. This helps to spread the plants, which increases plant diversity. This leads to an overall better environment.[131] A serious environmental problem is the decline of populations of pollinator insects, and a number of species of insects are now cultured primarily for pollination management in order to have sufficient pollinators in the field, orchard or greenhouse at bloom time.[132]:240–243 Another solution, as shown in Delaware, has been to raise native plants to help support native pollinators like *L. vierecki*.[133] Insects also produce useful substances such as honey, wax, lacquer and silk. Honey bees have been cultured by humans for thousands of years for honey, although contracting for crop pollination is becoming more significant for beekeepers. The silkworm has greatly affected human history, as silk-driven trade established relationships between China and the rest of the world.

Insectivorous insects, or insects that feed on other insects, are beneficial to humans if they eat insects that could cause damage to agriculture and human structures. For example, aphids feed on crops and cause problems for farmers, but ladybugs feed on aphids, and can be used as a means to significantly reduce pest aphid populations. While birds are perhaps more visible predators of insects, insects themselves account for the vast majority of insect consumption. Ants also help control animal populations by consuming small vertebrates.[134] Without predators to keep them in check, insects can undergo almost unstoppable population explosions.[33]:328–348[33]:400[135][136]

Insects are also used in medicine, for example fly larvae (maggots) were formerly used to treat wounds to prevent or stop gangrene, as they would only consume dead flesh. This treatment is finding modern usage in some hospitals. Recently insects have also gained attention as potential sources of drugs and other medicinal substances.[137] Adult insects, such as crickets and insect larvae of various kinds, are also commonly used as fishing bait.[138]

In research

Insects play important roles in biological research. For example, because of its small size, short generation time and high fecundity, the common fruit fly *Drosophila melanogaster* is a model organism for studies in the genetics of higher eukaryotes. *D. melanogaster* has been an essential part of studies into principles like genetic linkage, interactions between genes, chromosomal genetics, development, behavior and evolution. Because genetic systems are well conserved among eukaryotes, understanding basic cellular processes like DNA replication or transcription in fruit flies can help to understand those processes in other eukaryotes, including humans.[139] The genome of *D. melanogaster* was sequenced in 2000, reflecting the organism's important role in biological research. It was found that 70% of the fly genome is similar to the human genome, supporting the evolution theory.[140]



The common fruitfly *Drosophila melanogaster* is one of the most widely used organisms in biological research.

As food

In some cultures, insects, especially deep-fried cicadas, are considered to be delicacies, whereas in other places they form part of the normal diet. Insects have a high protein content for their mass, and some authors suggest their potential as a major source of protein in human nutrition.[33]:10–13 In most first-world countries, however, entomophagy (the eating of insects), is taboo.[141] Since it is impossible to entirely eliminate pest insects from the human food chain, insects are inadvertently present in many foods, especially grains. Food safety laws in many countries do not prohibit insect parts in food, but rather limit their quantity. According to cultural materialist anthropologist Marvin Harris, the eating of insects is taboo in cultures that have other protein sources such as fish or livestock.

Due to the abundance of insects and a worldwide concern of food shortages, the Food and Agriculture Organization of the United Nations considers that the world may have to, in the future, regard the prospects of eating insects as a food staple. Insects are noted for their nutrients, having a high content of protein, minerals and fats and are eaten by one-third of the global population.[142]

As pets

Many species of insects are sold and kept as pets.

In culture

Scarab beetles held religious and cultural symbolism in Old Egypt, Greece and some shamanistic Old World cultures. The ancient Chinese regarded cicadas as symbols of rebirth or immortality. In Mesopotamian literature, the epic poem of Gilgamesh has allusions to Odonata that signify the impossibility of immortality. Among the Aborigines of Australia of the Arrernte language groups, honey ants and witchety grubs served as personal clan totems. In the case of the 'San' bush-men of the Kalahari, it is the praying mantis that holds much cultural significance including creation and zen-like patience in waiting.[33]:9

See also

- Chemical ecology
- Defense in insects
- Entomology
- Ethnoentomology
- Flying and gliding animals
- Insect biodiversity
- Insect ecology
- Insect-borne diseases
- Prehistoric insects
- Pain in invertebrates

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Insect physiology

Insect physiology includes the physiology and biochemistry of insect organ systems.[1]

Although diverse, insects are quite similar in overall design, internally and externally. The insect is made up of three main body regions (tagmata), the head, thorax and abdomen. The head comprises six fused segments with compound eyes, ocelli, antennae and mouthparts, which differ according to the insect's particular diet, e.g. grinding, sucking, lapping and chewing. The thorax is made up of three segments: the pro, meso and meta thorax, each supporting a pair of legs which may also differ, depending on function, e.g. jumping, digging, swimming and running. Usually the middle and the last segment of the thorax have paired wings. The abdomen generally comprises eleven segments and contains the digestive and reproductive organs.[2] A general overview of the internal structure and physiology of the insect is presented, including digestive, circulatory, respiratory, muscular, endocrine and nervous systems, as well as sensory organs, temperature control, flight and molting.

Contents

Digestive system

Circulatory system

Respiratory system

Muscular system

Endocrine system

Nervous system
- Central nervous system
- Peripheral nervous system
- Sensory organs

Reproductive system
- Female
- Male
- Sexual and asexual reproduction

Life cycle

Moulting

References

External links

Digestive system

An insect uses its digestive system to extract nutrients and other substances from the food it consumes.[3] Most of this food is ingested in the form of macromolecules and other complex substances (such as proteins, polysaccharides, fats, and nucleic acids) which must be broken down by catabolic reactions into smaller molecules (i.e. amino acids, simple sugars, etc.) before being used by cells of the body for energy, growth, or reproduction. This break-down process is known as digestion.

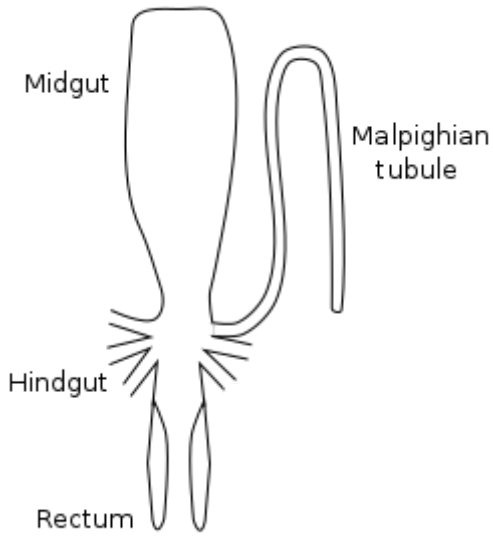
The insect's digestive system is a closed system, with one long enclosed coiled tube called the alimentary canal which runs lengthwise through the body. The alimentary canal only allows food to enter the mouth, and then gets processed as it travels toward the anus. The alimentary canal has specific sections for grinding and food storage, enzyme production, and nutrient

absorption.[2][4] Sphincters control the food and fluid movement between three regions. The three regions include the foregut (stomatodeum)(27,) the midgut (mesenteron)(13), and the hindgut (proctodeum)(16).

In addition to the alimentary canal, insects also have paired salivary glands and salivary reservoirs. These structures usually reside in the thorax (adjacent to the fore-gut). The salivary glands (30) produce saliva; the salivary ducts lead from the glands to the reservoirs and then forward through the head to an opening called the salivarium behind the hypopharynx; which movements of the mouthparts help mix saliva with food in the buccal cavity. Saliva mixes with food, which travels through salivary tubes into the mouth, beginning the process of breaking it down.[3][5]

The stomatedeum and proctodeum are invaginations of the epidermis and are lined with cuticle (intima). The mesenteron is not lined with cuticle but with rapidly dividing and therefore constantly replaced, epithelial cells.[2][4] The cuticle sheds with every moult along with the exoskeleton.[4] Food is moved down the gut by muscular contractions called peristalsis.[6]

1. **Stomatodeum** (foregut): This region stores, grinds and transports food to the next region.[7] Included in this are the buccal cavity, the pharynx, the oesophagus, the crop (stores food), and proventriculus or gizzard (grinds food).[4] Salivary secretions from the labial glands dilute the ingested food. In mosquitoes (Diptera), which are blood-feeding insects, anticoagulants and blood thinners are also released here.
2. **Mesenteron** (midgut): Digestive enzymes in this region are produced and secreted into the lumen and here nutrients are absorbed into the insect's body. Food is enveloped by this part of the gut as it arrives from the foregut by the peritrophic membrane which is a mucopolysaccharide layer secreted from the midgut's epithelial cells.[2] It is thought that this membrane prevents food pathogens from contacting the epithelium and attacking the insects' body.[2] It also acts as a filter allowing small molecules through, but preventing large molecules and particles of food from reaching the midgut cells.[7] After the large substances are broken down into smaller ones, digestion and consequent nutrient absorption takes place at the surface of the epithelium.[2] Microscopic projections from the mid-gut wall, called microvilli, increase surface area and allow for maximum absorption of nutrients.
3. **Proctodeum** (hindgut): This is divided into three sections; the anterior is the ileum, the middle portion, the colon, and the wider, posterior section is the rectum.[7] This extends from the pyloric valve which is located between the mid and the hindgut to the anus.[4] Here absorption of water, salts and other beneficial substances take place before excretion.[7] Like other animals, the removal of toxic metabolic waste requires water. However, for very small animals like insects, water conservation is a priority. Because of this, blind-ended ducts called Malpighian tubules come into play.[2] These ducts emerge as evaginations at the anterior end of the hindgut and are the main organs of osmoregulation and excretion.[4][7] These extract the waste products from the haemolymph, in which all the internal organs are bathed).[2] These tubules continually produce the insect's uric acid, which is transported to the hindgut, where important salts and water are re-absorbed by both the hindgut and rectum. Excrement is then voided as insoluble and non-toxic uric acid granules.[2] Excretion and osmoregulation in insects are not orchestrated by the Malpighian tubules alone, but require a joint function of the ileum and/or rectum.[7]



Stylised diagram of insect digestive tract showing Malpighian tubule (Orthopteran type)

Circulatory system

The main function of insect blood, hemolymph, is that of transport and it bathes the insect's body organs. Making up usually less than 25% of an insect's body weight, it transports hormones, nutrients and wastes and has a role in osmoregulation, temperature control, immunity, storage (water, carbohydrates and fats) and skeletal function. It also plays an essential part in the moulting process.[2][4] An additional role of the hemolymph in some orders, can be that of predatory defence. It can contain unpalatable and malodourous chemicals that will act as a deterrent to predators.[7]

Hemolymph contains molecules, ions and cells.[7] Regulating chemical exchanges between tissues, hemolymph is encased in the insect body cavity or haemocoel.[6][7] It is transported around the body by combined heart (posterior) and aorta (anterior) pulsations which are located dorsally just under the surface of the body.[2][4][7] It differs from vertebrate blood in that it doesn't contain any red blood cells and therefore is without high oxygen carrying capacity, and is more similar to lymph found in vertebrates.[6][7]

Body fluids enter through one way valved ostia which are openings situated along the length of the combined aorta and heart organ. Pumping of the hemolymph occurs by waves of peristaltic contraction, originating at the body's posterior end, pumping forwards into the dorsal vessel, out via the aorta and then into the head where it flows out into the haemocoel.[6][7] The hemolymph is circulated to the appendages unidirectionally with the aid of muscular pumps or accessory pulsatile organs which are usually found at the base of the antennae or wings and sometimes in the legs.[7] Pumping rate accelerates due to periods of increased activity.[4] Movement of hemolymph is particularly important for thermoregulation in orders such as Odonata, Lepidoptera, Hymenoptera and Diptera.[7]

Respiratory system

Insect respiration is accomplished without lungs using a system of internal tubes and sacs through which gases either diffuse or are actively pumped, delivering oxygen directly to tissues that need oxygen and eliminate carbon dioxide via their cells.[7] Since oxygen is delivered directly, the circulatory system is not used to carry oxygen, and is therefore greatly reduced; it has no closed vessels (i.e., no veins or arteries), consisting of little more than a single, perforated dorsal tube which pulses peristaltically, and in doing so helps circulate the hemolymph inside the body cavity.[7]

Air is taken in through spiracles, openings which are positioned laterally in the pleural wall, usually a pair on the anterior margin of the meso and meta thorax, and pairs on each of the eight or less abdominal segments, Numbers of spiracles vary from 1 to 10 pairs.[2][4][6][7] The oxygen passes through the tracheae to the tracheoles, and enters the body by the process of diffusion. Carbon dioxide leaves the body by the same process.[4]

The major tracheae are thickened spirally like a flexible vacuum hose to prevent them from collapsing and often swell into air sacs. Larger insects can augment the flow of air through their tracheal system, with body movement and rhythmic flattening of the tracheal air sacs.[4] Spiracles are closed and opened by means of valves and can remain partly or completely closed for extended periods in some insects, which minimises water loss.[2][4]

There are many different patterns of gas exchange demonstrated by different groups of insects. Gas exchange patterns in insects can range from continuous, diffusive ventilation, to discontinuous gas exchange.[7]

Terrestrial and a large proportion of aquatic insects perform gaseous exchange as previously mentioned under an open system. Other smaller numbers of aquatic insects have a closed tracheal system, for example, Odonata, Trichoptera, Ephemeroptera, which have tracheal gills and no functional spiracles. Endoparasitic larvae are without spiracles and also operate under a closed system. Here the tracheae separate peripherally, covering the general body surface which results in a cutaneous form of gaseous exchange. This peripheral tracheal division may also lie within the tracheal gills where gaseous exchange may also take place.[7]

Muscular system

Many insects are able to lift twenty times their own body weight like Rhinoceros beetle and may jump distances that are many times greater than their own length. This is because their energy output is high in relation to their body mass. [4][6]

The muscular system of insects ranges from a few hundred muscles to a few thousand.[4] Unlike vertebrates that have both smooth and striated muscles, insects have only striated muscles. Muscle cells are amassed into muscle fibers and then into the functional unit, the muscle.[6] Muscles are attached to the body wall, with attachment fibers running through the cuticle and to the epicuticle, where they can move different parts of the body including appendages such as wings.[4][7] The muscle fiber has many

cells with a plasma membrane and outer sheath or sarcolemma.[7] The sarcolemma is invaginated and can make contact with the tracheole carrying oxygen to the muscle fiber. Arranged in sheets or cylindrically, contractile myofibrils run the length of the muscle fiber. Myofibrils comprising a fine actin filament enclosed between a thick pair of myosin filaments slide past each other instigated by nerve impulses.[7]

Muscles can be divided into four categories:

1. **Visceral**: these muscles surround the tubes and ducts and produce peristalsis as demonstrated in the digestive system.[6]
2. **Segmental**: causing telescoping of muscle segments required for moulting, increase in body pressure and locomotion in legless larvae.[6]
3. **Appendicular**: originating from either the sternum or the tergum and inserted on the coxae these muscles move appendages as one unit.[6] These are arranged segmentally and usually in antagonistic pairs.[4] Appendage parts of some insects, e.g. the galea and the lacinia of the maxillae, only have flexor muscles. Extension of these structures is by haemolymph pressure and cuticle elasticity.[4]
4. **Flight**: Flight muscles are the most specialised category of muscle and are capable of rapid contractions. Nerve impulses are required to initiate muscle contractions and therefore flight. These muscles are also known as neurogenic or synchronous muscles. This is because there is a one-to-one correspondence between action potentials and muscle contractions. In insects with higher wing stroke frequencies the muscles contract more frequently than at the rate that the nerve impulse reaches them and are known as asynchronous muscles.[2][7]

Flight has allowed the insect to disperse, escape from enemies and environmental harm, and colonise new habitats.[2] One of the insect's key adaptations is flight, the mechanics of which differ from those of other flying animals because their wings are not modified appendages.[2][6] Fully developed and functional wings occur only in adult insects.[7] To fly, gravity and drag (air resistance to movement) have to be overcome.[7] Most insects fly by beating their wings and to power their flight they have either direct flight muscles attached to the wings, or an indirect system where there is no muscle-to-wing connection and instead they are attached to a highly flexible box-like thorax.[7]

Direct flight muscles generate the upward stroke by the contraction of the muscles attached to the base of the wing inside the pivotal point. Outside the pivotal point the downward stroke is generated through contraction of muscles that extend from the sternum to the wing. Indirect flight muscles are attached to the tergum and sternum. Contraction makes the tergum and base of the wing pull down. In turn this movement lever the outer or main part of the wing in strokes upward. Contraction of the second set of muscles, which run from the back to the front of the thorax, powers the downbeat. This deforms the box and lifts the tergum.[7]

Endocrine system

Hormones are the chemical substances that are transported in the insect's body fluids (haemolymph) that carry messages away from their point of synthesis to sites where physiological processes are influenced. These hormones are produced by glandular, neuroglandular and neuronal centres.[7] Insects have several organs that produce hormones, controlling reproduction, metamorphosis and moulting.[4] It has been suggested that a brain hormone is responsible for caste dermination in termites and diapause interruption in some insects.[4]

Four endocrine centers have been identified:

1. **Neurosecretory cells** in the brain can produce one or more hormones that affect growth, reproduction, homeostasis and metamorphosis.[4][7]
2. **Corpora cardiaca** are a pair of neuroglandular bodies that are found behind the brain and on either sides of the aorta. These not only produce their own neurohormones but they store and release other neurohormones including PTTH prothoracicotropic hormone (brain hormone), which stimulates the secretory activity of the prothoracic glands, playing an integral role in moulting.
3. **Prothoracic glands** are diffuse, paired glands located at the back of the head or in the thorax. These glands secrete an ecdysteroid called ecdysone, or the moulting hormone, which initiates the epidermal moulting process.[7] Additionally it plays a role in accessory reproductive glands in the female, differentiation of ovarioles and in the process of egg production.

4. **Corpora allata** are small, paired glandular bodies originating from the epithelium located on either side of the foregut. They secrete the juvenile hormone, which regulate reproduction and metamorphosis.[4][7]

Nervous system

Insects have a complex nervous system which incorporates a variety of internal physiological information as well as external sensory information.[7] As in the case of vertebrates, the basic component is the neuron or nerve cell. This is made up of a dendrite with two projections that receive stimuli and an axon, which transmits information to another neuron or organ, like a muscle. As for vertebrates, chemicals (neurotransmitters such as acetylcholine and dopamine) are released at synapses.[7]

Central nervous system

An insect's sensory, motor and physiological processes are controlled by the central nervous system along with the endocrine system.[7] Being the principal division of the nervous system, it consists of a brain, a ventral nerve cord and a subesophageal ganglion which is connected to the brain by two nerves, extending around each side of the oesophagus.

The brain has three lobes:

- **Protocerebrum**, innervating the compound eyes and the ocelli
- **Deutocerebrum**, innervating the antennae
- **Tritocerebrum**, innervating the foregut and the labrum.[4][7]

The ventral nerve cord extends from the suboesophageal ganglion posteriorly.[4] A layer of connective tissue called the neurolemma covers the brain, ganglia, major peripheral nerves and ventral nerve cords.

The head capsule (made up of six fused segments) has six pairs of ganglia. The first three pairs are fused into the brain, while the three following pairs are fused into the subesophageal ganglion.[7] The thoracic segments have one ganglion on each side, which are connected into a pair, one pair per segment. This arrangement is also seen in the abdomen but only in the first eight segments. Many species of insects have reduced numbers of ganglia due to fusion or reduction.[8] Some cockroaches have just six ganglia in the abdomen, whereas the wasp *Vespa crabro* has only two in the thorax and three in the abdomen. And some, like the house fly *Musca domestica*, have all the body ganglia fused into a single large thoracic ganglion. The ganglia of the central nervous system act as the coordinating centres with their own specific autonomy where each may coordinate impulses in specified regions of the insect's body.[4]

Peripheral nervous system

This consists of motor neuron axons that branch out to the muscles from the ganglia of the central nervous system, parts of the sympathetic nervous system and the sensory neurons of the cuticular sense organs that receive chemical, thermal, mechanical or visual stimuli from the insects environment.[7] The sympathetic nervous system includes nerves and the ganglia that innervate the gut both posteriorly and anteriorly, some endocrine organs, the spiracles of the tracheal system and the reproductive organs.[7]

Sensory organs

Chemical senses include the use of chemoreceptors, related to taste and smell, affecting mating, habitat selection, feeding and parasite-host relationships. Taste is usually located on the mouthparts of the insect but in some insects, such as bees, wasps and ants, taste organs can also be found on the antennae. Taste organs can also be found on the tarsi of moths, butterflies and flies. Olfactory sensilla enable insects to smell and are usually found in the antennae.[2] Chemoreceptor sensitivity related to smell in some substances, is very high and some insects can detect particular odours that are at low concentrations miles from their original source.[4]

Mechanical senses provide the insect with information that may direct orientation, general movement, flight from enemies, reproduction and feeding and are elicited from the sense organs that are sensitive to mechanical stimuli such as pressure, touch and vibration.[4] Hairs (setae) on the cuticle are responsible for this as they are sensitive to vibration touch and sound.[2]

Hearing structures or tympanal organs are located on different body parts such as, wings, abdomen, legs and antennae. These can respond to various frequencies ranging from 100 Hz to 240 kHz depending on insect species.[4] Many of the joints of the insect have tactile setae that register movement. Hair beds and groups of small hair like sensilla, determine proprioreception or information about the position of a limb, and are found on the cuticle at the joints of segments and legs. Pressure on the body wall or strain gauges are detected by the campiniform sensilla and internal stretch receptors sense muscle distension and digestive system stretching.[2][4]

The compound eye and the ocelli supply insect vision. The compound eye consists of individual light receptive units called ommatidia. Some ants may have only one or two, however dragonflies may have over 10,000. The more ommatidia the greater the visual acuity. These units have a clear lens system and light sensitive retina cells. By day, the image flying insects receive is made up of a mosaic of specks of differing light intensity from all the different ommatidia. At night or dusk, visual acuity is sacrificed for light sensitivity.[2] The ocelli are unable to form focused images but are sensitive mainly, to differences in light intensity.[4] Colour vision occurs in all orders of insects. Generally insects see better at the blue end of the spectrum than at the red end. In some orders sensitivity ranges can include ultraviolet.[2]

A number of insects have temperature and humidity sensors[2] and insects being small, cool more quickly than larger animals. Insects are generally considered cold-blooded or ectothermic, their body temperature rising and falling with the environment. However, flying insects raise their body temperature through the action of flight, above environmental temperatures.[4][6]

The body temperature of butterflies and grasshoppers in flight may be 5 °C or 10 °C above environmental temperature, however moths and bumblebees, insulated by scales and hair, during flight, may raise flight muscle temperature 20–30 °C above the environment temperature. Most flying insects have to maintain their flight muscles above a certain temperature to gain power enough to fly. Shivering, or vibrating the wing muscles allow larger insects to actively increase the temperature of their flight muscles, enabling flight.[4]

Until very recently, no one had ever documented the presence of nociceptors (the cells that detect and transmit sensations of pain) in insects,[9] though recent findings of nociception in larval fruit flies challenges this[10] and raises the possibility that some insects may be capable of feeling pain.

Reproductive system

Most insects have a high reproductive rate. With a short generation time, they evolve faster and can adjust to environmental changes more rapidly than other slower breeding animals.[2] Although there are many forms of reproductive organs in insects, there remains a basic design and function for each reproductive part. These individual parts may vary in shape (gonads), position (accessory gland attachment), and number (testicular and ovarian glands), with different insect groups.[7]

Female

The female insect's main reproductive function is to produce eggs, including the egg's protective coating, and to store the male spermatozoa until egg fertilisation is ready. The female reproductive organs include paired ovaries which empty their eggs (oocytes) via the calyces into lateral oviducts, joining to form the common oviduct. The opening (gonopore) of the common oviduct is concealed in a cavity called the genital chamber and this serves as a copulatory pouch (bursa copulatrix) when mating.[7] The external opening to this is the vulva. Often in insects the vulva is narrow and the genital chamber becomes pouch or tube like and is called the vagina. Related to the vagina is a saclike structure, the spermatheca, where spermatozoa are stored ready for egg fertilisation. A secretory gland nourishes the contained spermatozoa in the vagina.[4][4]

Egg development is mostly completed by the insect's adult stage and is controlled by hormones that control the initial stages of oogenesis and yolk deposition.[7] Most insects are oviparous, where the young hatch after the eggs have been laid.[4]

Insect sexual reproduction starts with sperm entry that stimulates oogenesis, meiosis occurs and the egg moves down the genital tract. Accessory glands of the female secrete an adhesive substance to attach eggs to an object and they also supply material that provides the eggs with a protective coating. Oviposition takes place via the female ovipositor.[4][6]

Male

The male's main reproductive function is to produce and store spermatozoa and provide transport to the reproductive tract of the female.[7] Sperm development is usually completed by the time the insect reaches adulthood.[4] The male has two testes, which contain follicles in which the spermatozoa are produced. These open separately into the sperm duct or vas deferens and this stores the sperm.[7] The vas deferentia then unite posteriorally to form a central ejaculatory duct, this opens to the outside on an aedeagus or a penis.[4] Accessory glands secrete fluids that comprise the spermatophore. This becomes a package that surrounds and carries the spermatozoa, forming a sperm-containing capsule.[4][7]

Sexual and asexual reproduction

Most insects reproduce via sexual reproduction, i.e. the egg is produced by the female, fertilised by the male and oviposited by the female. Eggs are usually deposited in a precise microhabitat on or near the required food.[6] However, some adult females can reproduce without male input. This is known as parthenogenesis and in the most common type of parthenogenesis the offspring are essentially identical to the mother. This is most often seen in aphids and scale insects.[6]

Life cycle

An insect's life-cycle can be divided into three types:

- **Ametabolous,** no metamorphosis, these insects are primitively wingless where the only difference between adult and nymph is size, e.g. order: Thysanura (silverfish).[4]
- **Hemimetabolous,** or incomplete metamorphosis. The terrestrial young are called nymphs and aquatic young are called naiads. Insect young are usually similar to the adult. Wings appear as buds on the nymphs or early instars. When the last moult is completed the wings expand to the full adult size, e.g. order: Odonata (dragonflies).
- **Holometabolus,** or complete metamorphosis. These insects have a different form in their immature and adult stages, have different behaviours and live in different habitats. The immature form is called larvae and remains similar in form but increases in size. They usually have chewing mouthparts even if the adult form mouth parts suck. At the last larval instar phase the insect forms into a pupa, it doesn't feed and is inactive, and here wing development is initiated, and the adult emerges e.g. order: Lepidoptera (butterflies and moths).[4]

Moulting

As an insect grows it needs to replace the rigid exoskeleton regularly.[2][4] Moulting may occur up to three or four times or, in some insects, fifty times or more during its life.[2] A complex process controlled by hormones, it includes the cuticle of the body wall, the cuticular lining of the tracheae, foregut, hindgut and endoskeletal structures.[2][4]

The stages of molting:

1. **Apolysis**—moulting hormones are released into the haemolymph and the old cuticle separates from the underlying epidermal cells. The epidermis increases in size due to mitosis and then the new cuticle is produced. Enzymes secreted by the epidermal cells digest the old endocuticle, not affecting the old sclerotised exocuticle.
2. **Ecdysis**—this begins with the splitting of the old cuticle, usually starting in the midline of the thorax's dorsal side. The rupturing force is mostly from haemolymph pressure that has been forced into thorax by abdominal muscle contractions caused by the insect swallowing air or water. After this the insect wriggles out of the old cuticle.

3. **Sclerotisation**—after emergence the new cuticle is soft and this a particularly vulnerable time for the insect as its hard protective coating is missing. After an hour or two the exocuticle hardens and darkens. The wings expand by the force of haemolymph into the wing veins.[2][4]

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Beekeeping

Beekeeping (or **apiculture**) is the maintenance of bee colonies, commonly in man-made hives, by humans. Most such bees are honey bees in the genus *Apis*, but other honey-producing bees such as *Melipona* stingless bees are also kept. A beekeeper (or apiarist) keeps bees in order to collect their honey and other products that the hive produce (including beeswax, propolis, flower pollen, bee pollen, and royal jelly), to pollinate crops, or to produce bees for sale to other beekeepers. A location where bees are kept is called an apiary or "bee yard".



Beekeeping, tacuinum sanitatis casanatensis (14th century)



Play media

Beekeeping in Serbia

Contents

History
- Early history
- Scientific study of honey bees
- Invention of the movable comb hive
- Evolution of hive designs
- Pioneers of practical and commercial beekeeping

Traditional beekeeping
- Fixed comb hives

Modern beekeeping
- Topbar hives
- Vertical stackable hives
- Protective clothing
- Smoker
- Effects of stings and of protective measures
- Natural beekeeping
- Urban or backyard beekeeping
- Indoor beekeeping

Bee colonies
- Species
- Castes
 - Mating of queens
 - Worker bees
 - Drones
- Differing stages of development
- Structure of a bee colony
- Annual cycle of a bee colony

Formation of new colonies
- Colony reproduction: swarming and supersedure
- Factors that trigger swarming
- Artificial swarming

Losses
- Diseases
- Parasites

Predators
World apiculture
Images of harvesting honey
See also
References
External links

History

Early history

Depictions of humans collecting honey from wild bees date to 10,000 years ago.[2] Beekeeping in pottery vessels began about 9,000 years ago in North Africa.[3] Domestication of bees is shown in Egyptian art from around 4,500 years ago.[4] Simple hives and smoke were used and honey was stored in jars, some of which were found in the tombs of pharaohs such as Tutankhamun. It wasn't until the 18th century that European understanding of the colonies and biology of bees allowed the construction of the moveable comb hive so that honey could be harvested without destroying the entire colony.



Honey seeker depicted on 8,000-year-old cave painting near Valencia, Spain[1]

At some point humans began to attempt to maintain colonies of wild bees in artificial hives made from hollow logs, wooden boxes, pottery vessels, and woven straw baskets or "skeps". Traces of beeswax are found in potsherds throughout the Middle East beginning about 7000 BCE.[3]

Honeybees were kept in Egypt from antiquity.[5] On the walls of the sun temple of Nyuserre Ini from the Fifth Dynasty, before 2422 BCE, workers are depicted blowing smoke into hives as they are removing honeycombs.[6] Inscriptions detailing the production of honey are found on the tomb of Pabasa from the Twenty-sixth Dynasty (c. 650 BCE), depicting pouring honey in jars and cylindrical hives.[7] Sealed pots of honey were found in the grave goods of pharaohs such as Tutankhamun.

> I am Shamash-resh-uṣur, the governor of Suhu and the land of Mari. Bees that collect honey, which none of my ancestors had ever seen or brought into the land of Suhu, I brought down from the mountain of the men of Habha, and made them settle in the orchards of the town 'Gabbari-built-it'. They collect honey and wax, and I know how to melt the honey and wax – and the gardeners know too. Whoever comes in the future, may he ask the old men of the town, (who will say) thus: "They are the buildings of Shamash-resh-uṣur, the governor of Suhu, who introduced honey bees into the land of Suhu."
>
> — translated text from stele, (Dalley, 2002)[8]



Stele showing Shamash-resh-uṣur praying to the gods Adad and Ishtar with an inscription about beekeeping in Babylonian cuneiform

In prehistoric Greece (Crete and Mycenae), there existed a system of high-status apiculture, as can be concluded from the finds of hives, smoking pots, honey extractors and other beekeeping paraphernalia in Knossos. Beekeeping was considered a highly valued industry controlled by beekeeping overseers—owners of gold rings depicting apiculture scenes rather than religious ones as they have been reinterpreted recently, contra Sir Arthur Evans.[9]

Archaeological finds relating to beekeeping have been discovered at Rehov, a Bronze and Iron Age archaeological site in the Jordan Valley, Israel.[10] Thirty intact hives, made of straw and unbaked clay, were discovered by archaeologist Amihai Mazar in the ruins of the city, dating from about 900 BCE. The hives were found in orderly rows, three high, in a manner that could have accommodated around 100 hives, held more than 1 million bees and had a potential annual yield of 500 kilograms of honey and 70 kilograms of beeswax, according to Mazar, and are evidence that an advanced honey industry existed in ancient Israel 3,000 years ago.[11][12][13]

In ancient Greece, aspects of the lives of bees and beekeeping are discussed at length by Aristotle. Beekeeping was also documented by the Roman writers Virgil, Gaius Julius Hyginus, Varro, and Columella.



The Beekeepers, 1568, by Pieter Bruegel the Elder

Beekeeping has also been practiced in ancient China since antiquity. In the book "Golden Rules of Business Success" written by Fan Li (or Tao Zhu Gong) during the Spring and Autumn period there are sections describing the art of beekeeping, stressing the importance of the quality of the wooden box used and how this can affect the quality of the honey. The Chinese word for honey (蜜 *mì*, reconstructed Old Chinese pronunciation *mjit) was borrowed from Indo-European proto-Tocharian language, the source of "honey", from proto-Tocharian **ḿət(ə)* (where **ḿ* is palatalized; cf. Tocharian B *mit*), cognate with English *mead*.

The ancient Maya domesticated a separate species of stingless bee. The use of stingless bees is referred to as meliponiculture, named after bees of the tribe Meliponini—such as *Melipona quadrifasciata* in Brazil. This variation of bee keeping still occurs around the world today.[14] For instance, in Australia, the stingless bee *Tetragonula carbonaria* is kept for production of their honey.[15]

Scientific study of honey bees

It was not until the 18th century that European natural philosophers undertook the scientific study of bee colonies and began to understand the complex and hidden world of bee biology. Preeminent among these scientific pioneers were Swammerdam, René Antoine Ferchault de Réaumur, Charles Bonnet, and François Huber. Swammerdam and Réaumur were among the first to use a microscope and dissection to understand the internal biology of honey bees. Réaumur was among the first to construct a glass walled observation hive to better observe activities within hives. He observed queens laying eggs in open cells, but still had no idea of how a queen was fertilized; nobody had ever witnessed the mating of a queen and drone and many theories held that queens were "self-fertile," while others believed that a vapor or "miasma" emanating from the drones fertilized queens without direct physical contact. Huber was the first to prove by observation and experiment that queens are physically inseminated by drones outside the confines of hives, usually a great distance away.

Following Réaumur's design, Huber built improved glass-walled observation hives and sectional hives that could be opened like the leaves of a book. This allowed inspecting individual wax combs and greatly improved direct observation of hive activity. Although he went blind before he was twenty, Huber employed a secretary, François Burnens, to make daily observations, conduct careful experiments, and keep accurate notes over more than twenty years. Huber confirmed that a hive consists of one queen who is the mother of all the female workers and male drones in the colony. He was also the first to confirm that mating with drones takes place outside of hives and that queens are inseminated by a number of successive matings with male drones,

high in the air at a great distance from their hive. Together, he and Burnens dissected bees under the microscope and were among the first to describe the ovaries and spermatheca, or sperm store, of queens as well as the penis of male drones. Huber is universally regarded as "the father of modern bee-science" and his "Nouvelles Observations sur Les Abeilles (or "New Observations on Bees") [16] revealed all the basic scientific truths for the biology and ecology of honeybees.

Invention of the movable comb hive


Rural beekeeping in the 16th century

Early forms of honey collecting entailed the destruction of the entire colony when the honey was harvested. The wild hive was crudely broken into, using smoke to suppress the bees, the honeycombs were torn out and smashed up — along with the eggs, larvae and honey they contained. The liquid honey from the destroyed brood nest was strained through a sieve or basket. This was destructive and unhygienic, but for hunter-gatherer societies this did not matter, since the honey was generally consumed immediately and there were always more wild colonies to exploit. But in settled societies the destruction of the bee colony meant the loss of a valuable resource; this drawback made beekeeping both inefficient and something of a "stop and start" activity. There could be no continuity of production and no possibility of selective breeding, since each bee colony was destroyed at harvest time, along with its precious queen.

During the medieval period abbeys and monasteries were centers of beekeeping, since beeswax was highly prized for candles and fermented honey was used to make alcoholic mead in areas of Europe where vines would not grow. The 18th and 19th centuries saw successive stages of a revolution in beekeeping, which allowed the bees themselves to be preserved when taking the harvest.

Intermediate stages in the transition from the old beekeeping to the new were recorded for example by Thomas Wildman in 1768/1770, who described advances over the destructive old skep-based beekeeping so that the bees no longer had to be killed to harvest the honey.[17] Wildman for example fixed a parallel array of wooden bars across the top of a straw hive or skep (with a separate straw top to be fixed on later) "so that there are in all seven bars of deal" [in a 10-inch-diameter (250 mm) hive] "to which the bees fix their combs".[18] He also described using such hives in a multi-storey configuration, foreshadowing the modern use of supers: he described adding (at a proper time) successive straw hives below, and eventually removing the ones above when free of brood and filled with honey, so that the bees could be separately preserved at the harvest for a following season. Wildman also described[19] a further development, using hives with "sliding frames" for the bees to build their comb, foreshadowing more modern uses of movable-comb hives. Wildman's book acknowledged the advances in knowledge of bees previously made by Swammerdam, Maraldi, and de Réaumur—he included a lengthy translation of Réaumur's account of the natural history of bees—and he also described the initiatives of others in designing hives for the preservation of bee-life when taking the harvest, citing in particular reports from Brittany dating from the 1750s, due to Comte de la Bourdonnaye. However, the forerunners of the modern hives with movable frames that are mainly used today are considered the traditional basket top bar (movable comb) hives of Greece, known as “Greek beehives”. The oldest testimony on their use dates back to 1669 although it is probable that their use is more than 3000 years old.[20]

The 19th century saw this revolution in beekeeping practice completed through the perfection of the movable comb hive by the American Lorenzo Lorraine Langstroth. Langstroth was the first person to make practical use of Huber's earlier discovery that there was a specific spatial measurement between the wax combs, later called *the bee space*, which bees do not block with wax, but keep as a free passage. Having determined this bee space (between 5 and 8 mm, or 1/4 to 3/8"), Langstroth then designed a series of wooden frames within a rectangular hive box, carefully maintaining the correct space between successive frames, and found that the bees would build parallel honeycombs in the box without bonding them to each other or to the hive walls. This enables the beekeeper to slide any frame out of the hive for inspection, without harming the bees or the comb, protecting the eggs, larvae and pupae contained within the cells. It also meant that combs containing honey could be gently removed and the honey



Lorenzo Langstroth (1810–1895)

extracted without destroying the comb. The emptied honey combs could then be returned to the bees intact for refilling. Langstroth's book, *The Hive and Honey-bee*, published in 1853, described his rediscovery of the bee space and the development of his patent movable comb hive.

The invention and development of the movable-comb-hive fostered the growth of commercial honey production on a large scale in both Europe and the US (see also Beekeeping in the United States).

Evolution of hive designs



Bees at the hive entrance

Langstroth's design for movable comb hives was seized upon by apiarists and inventors on both sides of the Atlantic and a wide range of moveable comb hives were designed and perfected in England, France, Germany and the United States. Classic designs evolved in each country: Dadant hives and Langstroth hives are still dominant in the US; in France the De-Layens trough-hive became popular and in the UK a British National hive became standard as late as the 1930s although in Scotland the smaller Smith hive is still popular. In some Scandinavian countries and in Russia the traditional trough hive persisted until late in the 20th century and is still kept in some areas. However, the Langstroth and Dadant designs remain ubiquitous in the US and also in many parts of Europe, though Sweden, Denmark, Germany, France and Italy all have their own national hive designs. Regional variations of hive evolved to reflect the climate, floral productivity and the reproductive characteristics of the various subspecies of native honey bee in each bio-region.

The differences in hive dimensions are insignificant in comparison to the common factors in all these hives: they are all square or rectangular; they all use movable wooden frames; they all consist of a floor, brood-box, honey super, crown-board and roof. Hives have traditionally been constructed of cedar, pine, or cypress wood, but in recent years hives made from injection molded dense polystyrene have become increasingly important.



Honey-laden honeycomb in a wooden frame

Hives also use queen excluders between the brood-box and honey supers to keep the queen from laying eggs in cells next to those containing honey intended for consumption. Also, with the advent in the 20th century of mite pests, hive floors are often replaced for part of (or the whole) year with a wire mesh and removable tray.

In 2015 the Flow Hive system was invented in Australia by Cedar Anderson and his father Stuart Anderson[21], allowing honey to be extracted without expensive centrifuge equipment.



Flow Hive 2 with honey pouring into jars

Pioneers of practical and commercial beekeeping

The 19th century produced an explosion of innovators and inventors who perfected the design and production of beehives, systems of management and husbandry, stock improvement by selective breeding, honey extraction and marketing. Preeminent among these innovators were:

Petro Prokopovych used frames with channels in the side of the woodwork; these were packed side by side in boxes that were stacked one on top of the other. The bees traveled from frame to frame and box to box via the channels. The channels were similar to the cut outs in the sides of modern wooden sections[22] (1814).

Jan Dzierżon was the father of modern apiology and apiculture. All modern beehives are descendants of his design.

François Huber did significant discoveries on the life of bees including the mating of queens and their interaction with other members of the hive in spite of his blindness. His work was published as *New Observations on the Natural History of Bees*.

L. L. Langstroth revered as the "father of American apiculture"; no other individual has influenced modern beekeeping practice more than Lorenzo Lorraine Langstroth. His classic book *The Hive and Honey-bee* was published in 1853.

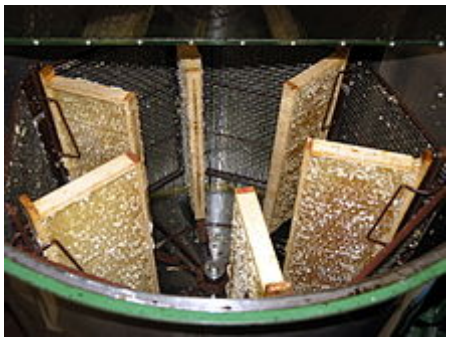
Moses Quinby often termed "the father of commercial beekeeping in the United States", author of *Mysteries of Bee-Keeping Explained*. He invented the Bee smoker in 1873.[23][24]

Amos Root author of the *A B C of Bee Culture*, which has been continuously revised and remains in print. Root pioneered the manufacture of hives and the distribution of bee-packages in the United States.

A. J. Cook author of *The Bee-Keepers' Guide; or Manual of the Apiary*, 1876.

Dr. C.C. Miller was one of the first entrepreneurs to actually make a living from apiculture. By 1878 he made beekeeping his sole business activity. His book, *Fifty Years Among the Bees*, remains a classic and his influence on bee management persists to this day.

Franz Hruschka was an Italian military officer who made one crucial invention that catalyzed the commercial honey industry. In 1865 he invented a simple machine for extracting honey from the comb by means of centrifugal force. His original idea was simply to support combs in a metal framework and then spin them around within a container to collect honey as it was thrown out by centrifugal force. This meant that honeycombs could be returned to a hive undamaged but empty, saving the bees a vast amount of work, time, and materials. This single invention greatly improved the efficiency of honey harvesting and catalysed the modern honey industry.[25]



Honey Extractor

Walter T. Kelley was an American pioneer of modern beekeeping in the early and mid-20th century. He greatly improved upon beekeeping equipment and clothing and went on to manufacture these items as well as other equipment. His company sold via catalog worldwide and his book, *How to Keep Bees & Sell Honey*, an introductory book of apiculture and marketing, allowed for a boom in beekeeping following World War II.

In the U.K. practical beekeeping was led in the early 20th century by a few men, pre-eminently Brother Adam and his Buckfast bee and R.O.B. Manley, author of many titles, including *Honey Production in the British Isles* and inventor of the Manley frame, still universally popular in the U.K. Other notable British pioneers include William Herrod-Hempsall and Gale.

Dr. Ahmed Zaky Abushady (1892–1955), was an Egyptian poet, medical doctor, bacteriologist and bee scientist who was active in England and in Egypt in the early part of the twentieth century. In 1919, Abushady patented a removable, standardized aluminum honeycomb. In 1919 he also founded The Apis Club in Benson, Oxfordshire, and its periodical Bee World, which was to be edited by Annie D. Betts and later by Dr. Eva Crane. The Apis Club was transitioned to the International Bee Research Association (IBRA). Its archives are held in the National Library of Wales. In Egypt in the 1930s, Abushady established The Bee Kingdom League and its organ, The Bee Kingdom.

In India, R. N. Mattoo was the pioneer worker in starting beekeeping with Indian honeybee, (*Apis cerana indica*) in the early 1930s. Beekeeping with European honeybee, (*Apis mellifera*) was started by Dr. A. S. Atwal and his team members, O. P. Sharma and N. P. Goyal in Punjab in the early 1960s. It remained confined to Punjab and Himachal Pradesh up to the late 1970s. Later on in 1982, Dr. R. C. Sihag, working at Haryana Agricultural University, Hisar (Haryana), introduced and established this honeybee in Haryana and standardized its management practices for semi-arid-subtropical climates. On the basis of these practices, beekeeping with this honeybee could be extended to the rest of the country. Now beekeeping with *Apis mellifera* predominates in India.

Traditional beekeeping

Fixed comb hives

A fixed comb hive is a hive in which the combs cannot be removed or manipulated for management or harvesting without permanently damaging the comb. Almost any hollow structure can be used for this purpose, such as a log gum, skep, wooden box, or a clay pot or tube. Fixed comb hives are no longer in common use in industrialized countries, and are illegal in places that require movable combs to inspect for problems such as varroa and American foulbrood. In many developing countries fixed comb hives are widely used and, because they can be made from any locally available material .



Wooden hives in Stripeikiai honeymaking museum, Lithuania

Beekeeping using fixed comb hives is an essential part of the livelihoods of many communities in poor countries. The charity Bees for Development recognizes that local skills to manage bees in fixed comb hives[26] are widespread in Africa, Asia, and South America. Internal size of fixed comb hives range from 32.7 liters (2000 cubic inches) typical of the clay tube hives used in Egypt to 282 liters (17209 cubic inches) for the Perone hive. Straw skeps, bee gums, and unframed box hives are unlawful in most US states, as the comb and brood cannot be inspected for diseases. However, skeps are still used for collecting swarms by hobbyists in the UK, before moving them into standard hives. Quinby used box hives to produce so much honey that he saturated the New York market in the 1860s. His writings contain excellent advice for management of bees in fixed comb hives.



Beekeeping at Kawah Ijen Mountain, Indonesia

Modern beekeeping

Topbar hives

Top bar hives have been widely adopted in Africa where they are used to keep tropical honeybee ecotypes. Their advantages include being light weight, adaptable, easy to harvest honey, and less stressful for the bees. Disadvantages include combs that are fragile and cannot usually be extracted and returned to the bees to be refilled and that they cannot easily be expanded for additional honey storage.

A growing number of amateur beekeepers are adopting various top-bar hives similar to the type commonly found in Africa. Top bar hives were originally used as a traditional beekeeping method in Greece and Vietnam with a history dating back over 2000 years.[13] These hives have no frames and the honey-filled comb is not returned after extraction. Because of this, the production of honey is likely to be somewhat less than that of a frame and super based hive such as Langstroth or Dadant. Top bar hives are

mostly kept by people who are more interested in having bees in their garden than in honey production per se. Some of the most well known top-bar hive designs are the Kenyan Top Bar Hive with sloping sides, the Tanzanian Top Bar Hive with straight sides, and Vertical Top Bar Hives, such as the Warre or "People's Hive" designed by Abbe Warre in the mid-1900s.

The initial costs and equipment requirements are typically much less than other hive designs. Scrap wood or #2 or #3 pine can often be used to build a nice hive. Top-bar hives also offer some advantages to interacting with the bees and the amount of weight that must be lifted is greatly reduced. Top-bar hives are being widely used in developing countries in Africa and Asia as a result of the Bees for Development program. Since 2011, a growing number of beekeepers in the U.S. are using various top-bar hives.[27]

Vertical stackable hives

There are three types of vertical stackable hives: hanging or top-access frame, sliding or side-access frame, and top bar.

Hanging frame hives include Langstroth, the British National, Dadant, Layens, and Rose, differing primarily by size or number of frames. The Langstroth was the first successful top-opened hive with movable frames. Many other hive designs are based on the principle of bee space first described by Langstroth, and is a descendant of Jan Dzierzon's Polish hive designs. Langstroth hives are the most common size in the United States and much of the world; the British National is the most common size in the United Kingdom; Dadant and Modified Dadant hives are widely used in France and Italy, and Layens by some beekeepers, where their large size is an advantage. Square Dadant hives–often called 12 frame Dadant or Brother Adam hives–are used in large parts of Germany and other parts of Europe by commercial beekeepers.

Any hanging frame hive design can be built as a sliding frame design. The AZ Hive, the original sliding frame design, integrates hives using Langstroth-sized frames into a honey house so as to streamline the workflow of honey harvest by localization of labor, similar to cellular manufacturing. The honey house can be a portable trailer, allowing the beekeeper to haul the hives to a site and provide pollination services.

Top bar stackable hives simply use top bars instead of full frames. The most common type is the Warre hive, although any hive with hanging frames can be made into a top bar stackable hive by using only the top bar and not the whole frame. This may work less-well with larger frames, where crosscomb and attachment can occur more-readily.

Protective clothing

Most beekeepers also wear some protective clothing. Novice beekeepers usually wear gloves and a hooded suit or hat and veil. Experienced beekeepers sometimes elect not to use gloves because they inhibit delicate manipulations. The face and neck are the most important areas to protect, so most beekeepers wear at least a veil. Defensive bees are attracted to the breath, and a sting on the face can lead to much more pain and swelling than a sting elsewhere, while a sting on a bare hand can usually be quickly removed by fingernail scrape to reduce the amount of venom injected.

The protective clothing is generally light colored (but not colorful) and of a smooth material. This provides the maximum differentiation from the colony's natural predators (such as bears and skunks) which tend to be dark-colored and furry.

'Stings' retained in clothing fabric continue to pump out an alarm pheromone that attracts aggressive action and further stinging attacks. Washing suits regularly, and rinsing gloved hands in vinegar minimizes attraction.

Smoker

Smoke is the beekeeper's third line of defense. Most beekeepers use a "smoker"—a device designed to generate smoke from the incomplete combustion of various fuels. Smoke calms bees; it initiates a feeding response in anticipation of possible hive abandonment due to fire.[28] Smoke also masks alarm pheromones released by guard bees or when bees are squashed in an

inspection. The ensuing confusion creates an opportunity for the beekeeper to open the hive and work without triggering a defensive reaction. In addition, when a bee consumes honey the bee's abdomen distends, supposedly making it difficult to make the necessary flexes to sting, though this has not been tested scientifically.

Many types of fuel can be used in a smoker as long as it is natural and not contaminated with harmful substances. These fuels include hessian, twine, burlap, pine needles, corrugated cardboard, and mostly rotten or punky wood. Indian beekeepers, especially in Kerala, often use coconut fibers as they are readily available, safe, and of negligible expense. Some beekeeping supply sources also sell commercial fuels like pulped paper and compressed cotton, or even aerosol cans of smoke. Other beekeepers use sumac as fuel because it ejects lots of smoke and doesn't have an odor.

Some beekeepers are using "liquid smoke" as a safer, more convenient alternative. It is a water-based solution that is sprayed onto the bees from a plastic spray bottle.

Torpor may also be induced by the introduction of chilled air into the hive – while chilled carbon dioxide may have harmful long-term effects.[29]



Beekeepers often wear protective clothing to protect themselves from stings

Effects of stings and of protective measures

Some beekeepers believe that the more stings a beekeeper receives, the less irritation each causes, and they consider it important for safety of the beekeeper to be stung a few times a season. Beekeepers have high levels of antibodies (mainly IgG) reacting to the major antigen of bee venom, phospholipase A2 (PLA).[30] Antibodies correlate with the frequency of bee stings.

The entry of venom into the body from bee-stings may also be hindered and reduced by protective clothing that allows the wearer to remove stings and venom sacs with a simple tug on the clothing. Although the stinger is barbed, a worker bee is less likely to become lodged into clothing than human skin.



Bee smoker with heat shield and hook

If a beekeeper is stung by a bee, there are many protective measures that should be taken in order to make sure the affected area does not become too irritated. The first cautionary step that should be taken following a bee sting is removing the stinger without squeezing the attached venom glands. A quick scrape with a fingernail is effective and intuitive. This step is effective in making sure that the venom injected does not spread, so the side effects of the sting will go away sooner. Washing the affected area with soap and water is also a good way to stop the spread of venom. The last step that needs to be taken is to apply ice or a cold compress to the stung area.[31]

Natural beekeeping

The natural beekeeping movement believes that bee hives are weakened by modern beekeeping and agricultural practices, such as crop spraying, hive movement, frequent hive inspections, artificial insemination of queens, routine medication, and sugar water feeding.

Practitioners of "natural beekeeping" tend to use variations of the top-bar hive, which is a simple design that retains the concept of having a movable comb without the use of frames or a foundation. The horizontal top-bar hive, as championed by Marty Hardison, Michael Bush, Philip Chandler, Dennis Murrell and others, can be seen as a modernization of hollow log hives, with

the addition of wooden bars of specific width from which bees hang their combs. Its widespread adoption in recent years can be attributed to the publication in 2007 of *The Barefoot Beekeeper*[32] by Philip Chandler, which challenged many aspects of modern beekeeping and offered the horizontal top-bar hive as a viable alternative to the ubiquitous Langstroth-style movable-frame hive.

The most popular vertical top-bar hive is the Warré hive, based on a design by the French priest Abbé Émile Warré (1867–1951) and popularized by Dr. David Heaf in his English translation of Warré's book *L'Apiculture pour Tous* as *Beekeeping For All*.[33]

Urban or backyard beekeeping



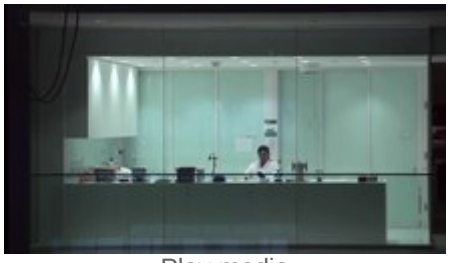
Honey bee in Toronto

Related to natural beekeeping, urban beekeeping is an attempt to revert to a less industrialized way of obtaining honey by utilizing small-scale colonies that pollinate urban gardens. Urban apiculture has undergone a renaissance in the first decade of the 21st century, and urban beekeeping is seen by many as a growing trend.

Some have found that "city bees" are actually healthier than "rural bees" because there are fewer pesticides and greater biodiversity in the urban gardens.[34] Urban bees may fail to find forage, however, and homeowners can use their landscapes to help feed local bee populations by planting flowers that provide nectar and pollen. An environment of year-round, uninterrupted bloom creates an ideal environment for colony reproduction.[35]

Urban beekeepers are testing modern types of beehives, testing for urban contest and ease of use. In 2015 the FlowHive appeared and in 2018 Beeing (https://beeing.it/en/home-your-bees-your-honey/), a hive made in Italy, that allows the beekeeper to extract honey without having contact with the bees.

Indoor beekeeping



Play media

MIT's "Synthetic Apiary" project raises colonies entirely indoors

Modern beekeepers have experimented with raising bees indoors, in a controlled environment or in indoor observation hives. This may be done for reasons of space and monitoring, or in the off-season. In the off-season, large commercial beekeepers may move colonies to "wintering" warehouses, with fixed temperature, light and humidity. This helps the bees remain healthy, but relatively dormant. These relatively dormant or "wintered" bees survive on stored honey, and new bees are not born.[36]

Experiments in raising bees for longer durations indoors have looked into more detailed and varying environment controls. In 2015, MIT's *Synthetic Apiary* project simulated springtime inside a closed environment, for a number of hives over the course of a winter. They provided food sources and simulated long days, and saw activity and reproduction levels comparable to the levels seen outdoors in warm weather. They concluded that such an indoor apiary could be sustained year-round if needed.[37][38]

Bee colonies

Species

There are more than 20,000 species of wild bees.[39] Many species are solitary[40] (e.g., mason bees, leafcutter bees (Megachilidae), carpenter bees and other ground-nesting bees). Many others rear their young in burrows and small colonies (e.g., bumblebees and stingless bees). Some honey bees are wild e.g. the little honeybee (*Apis florea*), giant honeybee (*Apis dorsata*)

and rock bee (*Apis laboriosa*). Beekeeping, or apiculture, is concerned with the practical management of the social species of honey bees, which live in large colonies of up to 100,000 individuals. In Europe and America the species universally managed by beekeepers is the Western honey bee (*Apis mellifera*). This species has several sub-species or regional varieties, such as the Italian bee (*Apis mellifera ligustica*), European dark bee (*Apis mellifera mellifera*), and the Carniolan honey bee (*Apis mellifera carnica*). In the tropics, other species of social bees are managed for honey production, including the Asiatic honey bee (*Apis cerana*).

Castes

A colony of bees consists of three castes of bee:

- a queen bee, which is normally the only breeding female in the colony;
- a large number of female worker bees, typically 30,000–50,000 in number;
- a number of male drones, ranging from thousands in a strong hive in spring to very few during dearth or cold season.


Queen bee (center)

The queen is the only sexually mature female in the hive and all of the female worker bees and male drones are her offspring. The queen may live for up to three years or more and may be capable of laying half a million eggs or more in her lifetime. At the peak of the breeding season, late spring to summer, a good queen may be capable of laying 3,000 eggs in one day, more than her own body weight. This would be exceptional however; a prolific queen might peak at 2,000 eggs a day, but a more average queen might lay just 1,500 eggs per day. The queen is raised from a normal worker egg, but is fed a larger amount of royal jelly than a normal worker bee, resulting in a radically different growth and metamorphosis. The queen influences the colony by the production and dissemination of a variety of pheromones or "queen substances". One of these chemicals suppresses the development of ovaries in all the female worker bees in the hive and prevents them from laying eggs.

Mating of queens

The queen emerges from her cell after 15 days of development and she remains in the hive for 3–7 days before venturing out on a mating flight. Mating flight is otherwise known as "nuptial flight". Her first orientation flight may only last a few seconds, just enough to mark the position of the hive. Subsequent mating flights may last from 5 minutes to 30 minutes, and she may mate with a number of male drones on each flight. Over several matings, possibly a dozen or more, the queen receives and stores enough sperm from a succession of drones to fertilize hundreds of thousands of eggs. If she does not manage to leave the hive to mate—possibly due to bad weather or being trapped in part of the hive—she remains infertile and becomes a *drone layer*, incapable of producing female worker bees. Worker bees sometimes kill a non-performing queen and produce another. Without a properly performing queen, the hive is doomed.

Mating takes place at some distance from the hive and often several hundred feet in the air; it is thought that this separates the strongest drones from the weaker ones, ensuring that only the fastest and strongest drones get to pass on their genes.

Worker bees

Most of the bees in a hive are female worker bees. At the height of summer when activity in the hive is frantic and work goes on non-stop, the life of a worker bee may be as short as 6 weeks; in late autumn, when no brood is being raised and no nectar is being harvested, a young bee may live for 16 weeks, right through the winter.

Over the course of their lives, worker bees' duties are dictated by age. For the first few weeks of their lifespan, they perform basic chores within the hive: cleaning empty brood cells, removing debris and other housekeeping tasks, making wax for building or repairing comb, and feeding larvae. Later, they may ventilate the hive or guard the entrance. Older workers leave the hive daily, weather permitting, to forage for nectar, pollen, water, and propolis.


Worker bee

Period	Work activity
Days 1–3	Cleaning cells and incubation
Day 3–6	Feeding older larvae
Day 6–10	Feeding younger larvae
Day 8–16	Receiving nectar and pollen from field bees
Day 12–18	Beeswax making and cell building
Day 14 onwards	Entrance guards; nectar, pollen, water and propolis foraging; robbing other hives

Drones

Drones are the largest bees in the hive (except for the queen), at almost twice the size of a worker bee. Note in the picture that they have much larger eyes than the workers have, presumably to better locate the queen during the mating flight. They do not work, do not forage for pollen or nectar, are unable to sting, and have no other known function than to mate with new queens and fertilize them on their mating flights. A bee colony generally starts to raise drones a few weeks before building queen cells so they can supersede a failing queen or prepare for swarming. When queen-raising for the season is over, bees in colder climates drive drones out of the hive to die, biting and tearing their legs and wings.


Larger drones compared to smaller workers

Differing stages of development

Stage of development	Queen	Worker	Drone
Egg	3 days	3 days	3 days
Larva (successive molts)	8 days	10 days	13 days
Cell Capped	day 8	day 8	day 10
Pupa	4 days	8 days	8 days
Total	15 days	21 days	24 days

Structure of a bee colony

A domesticated bee colony is normally housed in a rectangular hive body, within which eight to ten parallel frames house the vertical plates of honeycomb that contain the eggs, larvae, pupae and food for the colony. If one were to cut a vertical cross-section through the hive from side to side, the brood nest would appear as a roughly ovoid ball spanning 5–8 frames of comb. The two outside combs at each side of the hive tend to be exclusively used for long-term storage of honey and pollen.

Within the central brood nest, a single frame of comb typically has a central disk of eggs, larvae and sealed brood cells that may extend almost to the edges of the frame. Immediately above the brood patch an arch of pollen-filled cells extends from side to side, and above that again a broader arch of honey-filled cells extends to the frame tops. The pollen is protein-rich food for developing larvae, while honey is also food but largely energy rich rather than protein rich. The nurse bees that care for the developing brood secrete a special food called "royal jelly" after feeding themselves on honey and pollen. The amount of royal jelly fed to a larva determines whether it develops into a worker bee or a queen.

Apart from the honey stored within the central brood frames, the bees store surplus honey in combs above the brood nest. In modern hives the beekeeper places separate boxes, called "supers", above the brood box, in which a series of shallower combs is provided for storage of honey. This enables the beekeeper to remove some of the supers in the late summer, and to extract the surplus honey harvest, without damaging the colony of bees and its brood nest below. If all the honey is taken, including the amount of honey needed to survive winter, the beekeeper must replace these stores by feeding the bees sugar or corn syrup in autumn.

Annual cycle of a bee colony

The development of a bee colony follows an annual cycle of growth that begins in spring with a rapid expansion of the brood nest, as soon as pollen is available for feeding larvae. Some production of brood may begin as early as January, even in a cold winter, but breeding accelerates towards a peak in May (in the northern hemisphere), producing an abundance of harvesting bees synchronized to the main nectar flow in that region. Each race of bees times this build-up slightly differently, depending on how the flora of its original region blooms. Some regions of Europe have two nectar flows: one in late spring and another in late August. Other regions have only a single nectar flow. The skill of the beekeeper lies in predicting when the nectar flow will occur in his area and in trying to ensure that his colonies achieve a maximum population of harvesters at exactly the right time.

The key factor in this is the prevention or skillful management of the swarming impulse. If a colony swarms unexpectedly and the beekeeper does not manage to capture the resulting swarm, he is likely to harvest significantly less honey from that hive, since he has lost half his worker bees at a single stroke. If, however, he can use the swarming impulse to breed a new queen but keep all the bees in the colony together, he maximizes his chances of a good harvest. It takes many years of learning and experience to be able to manage all these aspects successfully, though owing to variable circumstances many beginners often achieve a good honey harvest.

Formation of new colonies

Colony reproduction: swarming and supersedure

All colonies are totally dependent on their queen, who is the only egg-layer. However, even the best queens live only a few years and one or two years longevity is the norm. She can choose whether or not to fertilize an egg as she lays it; if she does so, it develops into a female worker bee; if she lays an unfertilized egg it becomes a male drone. She decides which type of egg to lay depending on the size of the open brood cell she encounters on the comb. In a small worker cell, she lays a fertilized egg; if she finds a larger drone cell, she lays an unfertilized drone egg.



A swarm about to land

All the time that the queen is fertile and laying eggs she produces a variety of pheromones, which control the behavior of the bees in the hive. These are commonly called *queen substance*, but there are various pheromones with different functions. As the queen ages, she begins to run out of stored sperm, and her pheromones begin to fail.

Inevitably, the queen begins to falter, and the bees decide to replace her by creating a new queen from one of her worker eggs. They may do this because she has been damaged (lost a leg or an antenna), because she has run out of sperm and cannot lay fertilized eggs (has become a "drone laying queen"), or because her pheromones have dwindled to where they cannot control all the bees in the hive. At this juncture, the bees produce one or more queen cells by modifying existing worker cells that contain a normal female egg. They then pursue one of two ways to replace the queen: **supersedure**, replacing or superseding the queen without swarming, or **swarm cell production**, dividing the hive into two colonies through swarming.

Supersedure is highly valued as a behavioral trait by beekeepers. A hive that supersedes its old queen does not lose any stock. Instead it creates a new queen and the old one fades away or is killed when the new queen emerges. In these hives, the bees produce just one or two queen cells, characteristically in the center of the face of a broodcomb.

Swarm cell production involves creating many queen cells, typically a dozen or more. These are located around the edges of a broodcomb, often at the sides and the bottom.

Once either process has begun, the old queen leaves the hive with the hatching of the first queen cells. She leaves accompanied by a large number of bees, predominantly young bees (wax-secretors), who form the basis of the new hive. Scouts are sent out from the swarm to find suitable hollow trees or rock crevices. As soon as one is found, the entire swarm moves in. Within a matter of hours, they build new wax brood combs, using honey stores that the young bees have filled themselves with before leaving the old hive. Only young bees can secrete wax from special abdominal segments, and this is why swarms tend to contain more young bees. Often a number of virgin queens accompany the first swarm (the "prime swarm"), and the old queen is replaced as soon as a daughter queen mates and begins laying. Otherwise, she is quickly superseded in the new home.



New wax combs between basement joists

Different sub-species of *Apis mellifera* exhibit differing swarming characteristics. In general the more northerly black races are said to swarm less and supersede more, whereas the more southerly yellow and grey varieties are said to swarm more frequently. The truth is complicated because of the prevalence of cross-breeding and hybridization of the sub species.

Factors that trigger swarming

Some beekeepers may monitor their colonies carefully in spring and watch for the appearance of queen cells, which are a dramatic signal that the colony is determined to swarm.



A swarm attached to a branch

This swarm looks for shelter. A beekeeper may capture it and introduce it into a new hive, helping meet this need. Otherwise, it returns to a feral state, in which case it finds shelter in a hollow tree, excavation, abandoned chimney, or even behind shutters.

A small after-swarm has less chance of survival and may threaten the original hive's survival if the number of individuals left is unsustainable. When a hive swarms despite the beekeeper's preventative efforts, a good management practice is to give the reduced hive a couple frames of open brood with eggs. This helps replenish the hive more quickly and gives a second opportunity to raise a queen if there is a mating failure.

Each race or sub-species of honey bee has its own swarming characteristics. Italian bees are very prolific and inclined to swarm; Northern European black bees have a strong tendency to supersede their old queen without swarming. These differences are the result of differing evolutionary pressures in the regions where each sub-species evolved.

Artificial swarming

When a colony accidentally loses its queen, it is said to be "queenless". The workers realize that the queen is absent after as little as an hour, as her pheromones fade in the hive. Instinctively, the workers select cells containing eggs aged less than three days and enlarge these cells dramatically to form "emergency queen cells". These appear similar to large peanut-like structures about an inch long that hang from the center or side of the brood combs. The developing larva in a queen cell is fed differently from an ordinary worker-bee; in addition to the normal honey and pollen, she receives a great deal of royal jelly, a special food secreted by young "nurse bees" from the hypopharyngeal gland. This special food dramatically alters the growth and development of the larva so that, after metamorphosis and pupation, it emerges from the cell as a queen bee. The queen is the only bee in a colony which has fully developed ovaries, and she secretes a pheromone which suppresses the normal development of ovaries in all her workers.

Beekeepers use the ability of the bees to produce new queens to increase their colonies in a procedure called *splitting a colony*. To do this, they remove several brood combs from a healthy hive, taking care to leave the old queen behind. These combs must contain eggs or larvae less than three days old and be covered by young *nurse bees*, which care for the brood and keep it warm. These brood combs and attendant nurse bees are then placed into a small "nucleus hive" with other combs containing honey and pollen. As soon as the nurse bees find themselves in this new hive and realize they have no queen, they set about constructing emergency queen cells using the eggs or larvae they have in the combs with them.

Losses

Diseases

The common agents of disease that affect adult honey bees include fungi, bacteria, protozoa, viruses, parasites, and poisons. The gross symptoms displayed by affected adult bees are very similar, whatever the cause, making it difficult for the apiarist to ascertain the causes of problems without microscopic identification of microorganisms or chemical analysis of poisons.[41] Since 2006 colony losses from colony collapse disorder have been increasing across the world although the causes of the syndrome are, as yet, unknown.[42][43] In the US, commercial beekeepers have been increasing the number of hives to deal with higher rates of attrition.[44]

Parasites

Galleria mellonella and *Achroia grisella* “wax moth” larvae that hatch, tunnel through, and destroy comb that contains bee larvae and their honey stores. The tunnels they create are lined with silk, which entangles and starves emerging bees. Destruction of honeycombs also results in honey leaking and being wasted. A healthy hive can manage wax moths, but weak colonies, unoccupied hives, and stored frames can be decimated.[45]

Small hive beetle *(Aethina tumida)* is native to Africa but has now spread to most continents. It is a serious pest among honey bees unadapted to it.[46]

Varroa destructor, the Varroa mite, is an established pest of two species of honey bee through many parts of the world, and is blamed by many researchers as a leading cause of CCD.[47]

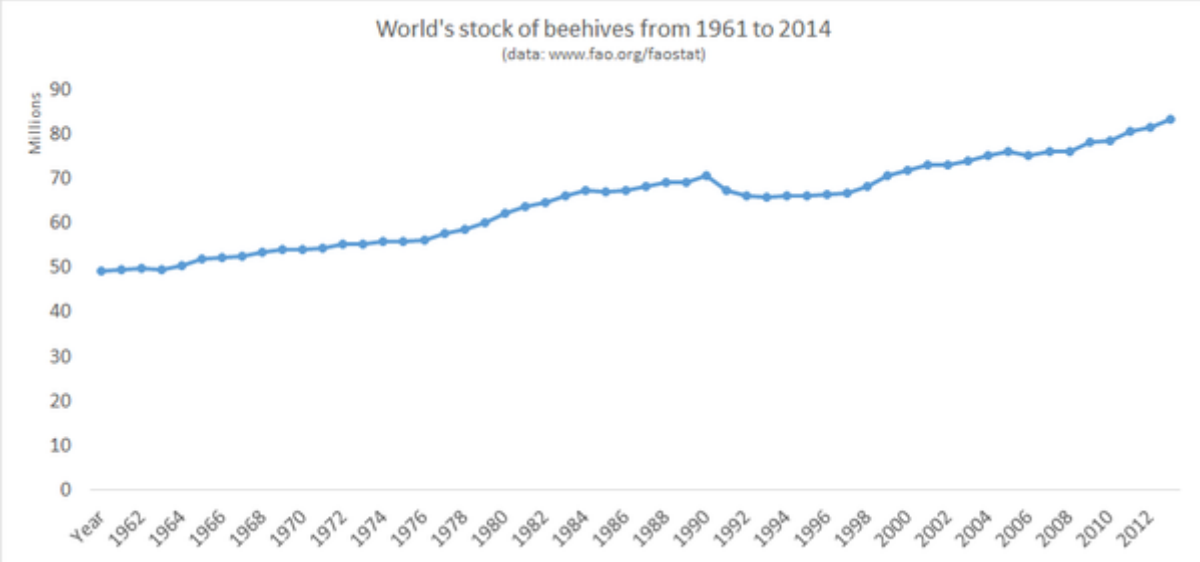
Acarapis woodi, the tracheal mite, infests the trachea of honey bees.

Predators

Most predators prefer not to eat honeybees due to their unpleasant sting, but they still have some predators. These include large animals such as skunks or bears, which are after the honey and brood in the nest as well as the adult bees themselves.[48] Some birds will also eat bees (for example, bee-eaters, which are named for their bee-centric diet), as do some robber flies, such as *Mallophora ruficauda*, which is a pest of apiculture in South America due to its habit of eating workers while they are foraging in meadows.[49]

World apiculture

According to U.N. FAO data (http://www.fao.org/faostat), the world's beehive stock rose from around 50 million in 1961 to around 83 million in 2014, which comes to about 1.3% average annual growth. Average annual growth has accelerated to 1.9% since 2009.



World's stock of beehives from 1961 to 2014

Sericulture

Sericulture, or **silk farming**, is the cultivation of silkworms to produce silk. Although there are several commercial species of silkworms, *Bombyx mori* (the caterpillar of the domestic silkmoth) is the most widely used and intensively studied silkworm. Silk was believed to have first been produced in China as early as the Neolithic Period. Sericulture has become an important cottage industry in countries such as Brazil, China, France, India, Italy, Japan, Korea, and Russia. Today, China and India are the two main producers, with more than 60% of the world's annual production.



Court Ladies Preparing Newly Woven Silk by Emperor Huizong of Song

Contents

History

Production

Stages of production

See also

References

External links



Silkworm and cocoon

History

According to OMKAR text, the discovery of silk production dates to about 2700 BC, although archaeological records point to silk cultivation as early as the Yangshao period (5000–3000 BC).[1] In 1977, a piece of ceramic created 5400–5500 years ago and designed to look like a silkworm was discovered in Nancun, Hebei, providing the earliest known evidence of sericulture.[2] Also, by careful analysis of archaeological silk fibre found on Indus Civilization sites dating back to 2450–2000 BC, it is believed that silk was being used over a wide region of South Asia.[3][4] By about the first half of the 1st century AD, it had reached ancient Khotan,[5] by a series of interactions along the Silk Road. By AD 140, the practice had been established in India.[6] In the 6th century AD, the smuggling of silkworm eggs into the Byzantine Empire led to its establishment in the Mediterranean, remaining a monopoly in the Byzantine Empire for centuries (Byzantine silk). In 1147, during the Second Crusade, Roger II of Sicily (1095–1154) attacked Corinth and Thebes, two important centres of Byzantine silk production, capturing the weavers and their equipment and establishing his own silkworks in Palermo and Calabria,[7] eventually spreading the industry to Western Europe.

Chinese sericulture process



The silkworms and mulberry leaves are placed on trays.



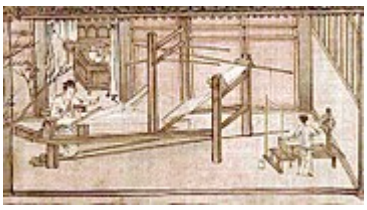
Twig frames for the silkworms are prepared.



The cocoons are weighed.



The cocoons are soaked and the silk is wound on spools.



The silk is woven using a loom.

Production

The silkworms are fed with mulberry leaves, and after the fourth moult, they climb a twig placed near them and spin their silken cocoons. The silk is a continuous filament comprising fibroin protein, secreted from two salivary glands in the head of each worm, and a gum called sericin, which cements the filaments. The sericin is removed by placing the cocoons in hot water, which frees the silk filaments and readies them for reeling. This is known as the degumming process.[8] The immersion in hot water also kills the silkmoth pupa.

Single filaments are combined to form thread, which is drawn under tension through several guides and wound onto reels. The threads may be plied to form yarn. After drying, the raw silk is packed according to quality.

Stages of production

The stages of production are as follows:

1. The female silkmoth lays 300 to 500 eggs.
2. The silkmoth eggs hatch to form larvae or caterpillars, known as silkworms.
3. The larvae feed on mulberry leaves.
4. Having grown and moulted several times, the silkworm extrudes a silk fibre and forms a net to hold itself.
5. It swings itself from side to side in a figure '8', distributing the saliva that will form silk.
6. The silk solidifies when it contacts the air.
7. The silkworm spins approximately one mile of filament and completely encloses itself in a cocoon in about two or three days. The amount of usable quality silk in each cocoon is small. As a result, about 2,500 silkworms are required to produce a pound of raw silk.[9]
8. The intact cocoons are boiled, killing the silkworm pupa.
9. The silk is obtained by brushing the undamaged cocoon to find the outside end of the filament.
10. The silk filaments are then wound on a reel. One cocoon contains approximately 1,000 yards of silk filament. The silk at this stage is known as raw silk. One thread comprises up to 48 individual silk filaments.

Mahatma Gandhi was critical of silk production based on the Ahimsa philosophy "not to hurt any living thing". He also promoted "Ahimsa silk", made without boiling the pupa to procure the silk and wild silk made from the cocoons of wild and semiwild silkmoths.[10][11] The Human League also criticised sericulture in their early single "Being Boiled". In the early 21st century, the

organisation PETA has also campaigned against silk.[12]



The third stage of the silkworm



Silkworms on a modern rotary mountage



Silk cocoons on mountages



Play media

A silk pavilion constructed with silkworms

See also

- Good agricultural practices
- Macclesfield silk museums
- Magnanery
- Silk industry in Azerbaijan
- Silk industry in China

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Shellac

Shellac is a resin secreted by the female lac bug, on trees in the forests of India and Thailand. It is processed and sold as dry flakes (pictured) and dissolved in alcohol to make liquid shellac, which is used as a brush-on colorant, food glaze and wood finish. Shellac functions as a tough natural primer, sanding sealant, tannin-blocker, odour-blocker, stain, and high-gloss varnish. Shellac was once used in electrical applications as it possesses good insulation qualities and it seals out moisture. Phonograph and 78 rpm gramophone records were made of it until they were replaced by vinyl long-playing records from the 1950s onwards.



Some of the many different colors of shellac

From the time it replaced oil and wax finishes in the 19th century, shellac was one of the dominant wood finishes in the western world until it was largely replaced by nitrocellulose lacquer in the 1920s and 1930s.



Shellac in alcohol

Contents

Etymology

Production

Colours and availability

Properties

History

Uses

- Historical
- Current
 - Other

Gallery

References

External links

Etymology

Shellac comes from *shell* and *lac*, a calque of French *laque en écailles*, "lac in thin pieces", later *gomme-laque*, "gum lac".[1] Most European languages (except Romance ones and Greek) have borrowed the word for the substance from English or from the German equivalent *Schellack*.

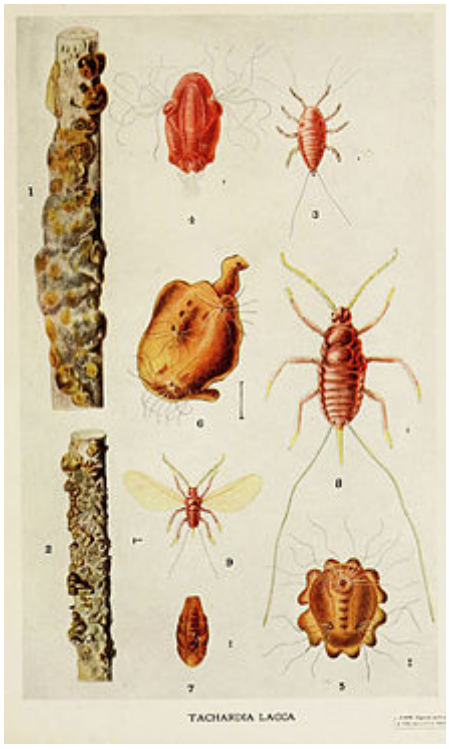
Production

Shellac is scraped from the bark of the trees where the female lac bug, *Kerria lacca* (order Hemiptera, family Kerriidae, also known as *Laccifer lacca*), secretes it to form a tunnel-like tube as it traverses the branches of the tree. Though these tunnels are sometimes referred to as "cocoons", they are not cocoons in the entomological sense.[2] This insect is in the same superfamily as the insect from which cochineal is obtained. The insects suck the sap of the tree and excrete "sticklac" almost constantly. The least-coloured shellac is produced when the insects feed on the kusum tree (*Schleichera*).



Lac tubes created by *Kerria lacca*

The number of lac bugs required to produce 1 kilogram (2.2 lb) of shellac has variously been estimated as 50,000,[3] 200,000,[4] or 300,000.[5][6] The root word lakh is a unit in Indian numbering system for 100,000 and presumably refers to the huge numbers of insects that swarm on host trees, up to 150 per square inch.[7]



Drawing of the insect *Kerria lacca* and its shellac tubes, by Harold Maxwell-Lefroy, 1909

The raw shellac, which contains bark shavings and lac bugs removed during scraping, is placed in canvas tubes (much like long socks) and heated over a fire. This causes the shellac to liquefy, and it seeps out of the canvas, leaving the bark and bugs behind. The thick, sticky shellac is then dried into a flat sheet and broken into flakes, or dried into "buttons" (pucks/cakes), then bagged and sold. The end-user then crushes it into a fine powder and mixes it with ethyl alcohol before use, to dissolve the flakes and make liquid shellac.

Liquid shellac has a limited shelf life (about 1 year), so is sold in dry form for dissolution before use. Liquid shellac sold in hardware stores is often marked with the production (mixing) date, so the consumer can know whether the shellac inside is still good. Some manufacturers (e.g., Zinsser) have ceased labeling shellac with the production date, but the production date may be discernible from the production lot code. Alternatively, old shellac may be tested to see if it is still usable: a few drops on glass should quickly dry to a hard surface. Shellac that remains tacky for a long time is no longer usable. Storage life depends on peak temperature, so refrigeration extends shelf life.

The thickness (concentration) of shellac is measured by the unit "pound cut", referring to the amount (in pounds) of shellac flakes dissolved in a gallon of denatured alcohol. For example: a 1-lb. cut of shellac is the strength obtained by dissolving one pound of shellac flakes in a gallon of alcohol.[8] Most pre-mixed commercial preparations come at a 3-lb. cut. Multiple thin layers of shellac produce a significantly better end result than a few thick layers. Thick layers of shellac do not adhere to the substrate or to each other well, and thus can peel off with relative ease; in addition, thick shellac will obscure fine details in carved designs in wood and other substrates.

Shellac naturally dries to a high-gloss sheen. For applications where a flatter (less shiny) sheen is desired, products containing amorphous silica,[9] such as "Shellac Flat", may be added to the dissolved shellac.

Shellac naturally contains a small amount of wax (3%–5% by volume), which comes from the lac bug. In some preparations, this wax is removed (the resulting product being called "dewaxed shellac"). This is done for applications where the shellac will be coated with something else (such as paint or varnish), so the topcoat will adhere. Waxy (non-dewaxed) shellac appears milky in liquid form, but dries clear.

Colours and availability

Shellac comes in many warm colours, ranging from a very light blonde ("platina") to a very dark brown ("garnet"), with many varieties of brown, yellow, orange and red in between. The colour is influenced by the sap of the tree the lac bug is living on and by the time of harvest. Historically, the most commonly sold shellac is called "orange shellac", and was used extensively as a combination stain and protectant for wood panelling and cabinetry in the 20th century.

Shellac was once very common anywhere paints or varnishes were sold (such as hardware stores). However, cheaper and more abrasion- and chemical-resistant finishes, such as polyurethane, have almost completely replaced it in decorative residential wood finishing such as hardwood floors, wooden wainscoting plank panelling, and kitchen cabinets. These alternative products, however, must be applied over a stain if the user wants the wood to be coloured; clear or blonde shellac may be applied over a stain without affecting the colour of the finished piece, as a protective topcoat. "Wax over shellac" (an application of buffed-on paste wax over several coats of shellac) is often regarded as a beautiful, if fragile, finish for hardwood floors. Luthiers still use shellac to *French polish* fine acoustic stringed instruments, but it has been replaced by synthetic plastic lacquers and varnishes in many workshops, especially high-volume production environments.[10]

Shellac dissolved in alcohol, typically more dilute than French-Polish, is now commonly sold as "sanding sealer" by several companies. It is used to seal wooden surfaces, often as preparation for a final more durable finish; it reduces the amount of final coating required by reducing its absorption into the wood.

Properties

Shellac is a natural bioadhesive polymer and is chemically similar to synthetic polymers, and thus can be considered a natural form of plastic. It can be turned into a moulding compound when mixed with wood flour and moulded under heat and pressure methods, so it can also be classified as thermoplastic.



A decorative medal made in France in the early 20th century moulded from shellac compound, the same used for phonograph records of the period

Shellac scratches more easily than most lacquers and varnishes, and application is more labour-intensive, which is why it has been replaced by plastic in most areas. But damaged shellac can easily be touched up with another coat of shellac (unlike polyurethane) because the new coat merges with and bonds to the existing coat(s). Shellac is much softer than Urushi lacquer, for instance, which is far superior with regard to both chemical and mechanical resistance.

Shellac is soluble in alkaline solutions such as ammonia, sodium borate, sodium carbonate, and sodium hydroxide, and also in various organic solvents. When dissolved in de-natured alcohol or ethanol, shellac yields a coating of good durability and hardness.

Upon mild hydrolysis shellac gives a complex mix of aliphatic and alicyclic hydroxy acids and their polymers that varies in exact composition depending upon the source of the shellac and the season of collection. The major component of the aliphatic component is aleuritic acid, whereas the main alicyclic component is shellolic acid.[11]

Shellac is UV-resistant, and does not darken as it ages (though the wood under it may do so, as in the case of pine).[4]

History

The earliest written evidence of shellac goes back 3,000 years, but shellac is known to have been used earlier.[4] According to the ancient Indian epic poem, the Mahabharata, an entire palace was built out of dried shellac.[4]

Shellac was in rare use as a dyestuff for as long as there was a trade with the East Indies. Merrifield[12] cites 1220 for the introduction of shellac as an artist's pigment in Spain. Lapis lazuli, an ultramarine pigment from Afghanistan, was already being imported long before this.

The use of overall paint or varnish decoration on large pieces of furniture was first popularised in Venice (then later throughout Italy). There are a number of 13th-century references to painted or varnished cassone, often dowry cassone that were made deliberately impressive as part of dynastic marriages. The definition of varnish is not always clear, but it seems to have been a spirit varnish based on gum benjamin or mastic, both traded around the Mediterranean. At some time, shellac began to be used as well. An article from the *Journal of the American Institute of Conservation* describes using infrared spectroscopy to identify shellac coating on a 16th-century cassone.[13] This is also the period in history where "varnisher" was identified as a distinct trade, separate from both carpenter and artist.

Another use for shellac is sealing wax. Woods's *The Nature and Treatment of Wax and Shellac Seals*[14] discusses the various formulations, and the period when shellac started to be added to the previous beeswax recipes.

The "period of widespread introduction" would seem to be around 1550 to 1650, when the substance moved from being a rarity on highly decorated pieces to being described in the standard texts of the day.

Uses

Historical

In the early- and mid-twentieth century, orange shellac was used as a one-product finish (combination stain and varnish-like topcoat) on decorative wood panelling used on walls and ceilings in homes, particularly in the US. In the American South, use of knotty pine plank panelling covered with orange shellac was once as common in new construction as drywall is today. It was also often used on kitchen cabinets and hardwood floors, prior to the advent of polyurethane.

Until the advent of vinyl, most gramophone records were pressed from shellac compounds.[15][16] From 1921 to 1928, 18,000 tons of shellac were used to create 260 million records for Europe.[7] In the 1930s, it was estimated that half of all shellac was used for gramophone records.[17] Use of shellac for records was common until the 1950s and continued into the 1970s in some non-Western countries.

Until recent advances in technology, shellac (French polish) was the only glue used in the making of ballet dancers' pointe shoes, to stiffen the box (toe area) to support the dancer en pointe. Many manufacturers of pointe shoes still use the traditional techniques, and many dancers use shellac to revive a softening pair of shoes.[18]

Shellac was historically used as a protective coating on paintings.

Sheets of Braille were coated with shellac to help protect them from wear due to being read by hand.

Shellac was used from the mid-nineteenth century to produce small moulded goods such as picture frames, boxes, toilet articles, jewelry, inkwells and even dentures. Advances in plastics have rendered shellac obsolete as a moulding compound.

Shellac (both orange and white varieties) was used both in the field and laboratory to glue and stabilise dinosaur bones until about the mid-1960s. While effective at the time, the long-term negative effects of shellac (being organic in nature) on dinosaur bones and other fossils is debated, and shellac is very rarely used by professional conservators and fossil preparators today.

Shellac was used for fixing inductor, motor, generator and transformer windings. It was applied directly to single-layer windings in an alcohol solution. For multi-layer windings, the whole coil was submerged in shellac solution, then drained and placed in a warm place to allow the alcohol to evaporate. The shellac locked the wire turns in place, provided extra insulation, prevented

movement and vibration and reduced buzz and hum. In motors and generators it also helps transfer force generated by magnetic attraction and repulsion from the windings to the rotor or armature. In more recent times, shellac has been replaced in these applications by synthetic resins such as polyester resin. Some applications use shellac mixed with other natural or synthetic resins, such as pine resin or phenol-formaldehyde resin, of which Bakelite is the best known, for electrical use. Mixed with other resins, barium sulfate, calcium carbonate, zinc sulfide, aluminium oxide and/or cuprous carbonate (malachite), shellac forms a component of heat-cured capping cement used to fasten the caps or bases to the bulbs of electric lamps.

Current

It is the central element of the traditional "French polish" method of finishing furniture, fine string instruments, and pianos.

Shellac, edible, is used as a glazing agent on pills (see excipient) and sweets, in the form of *pharmaceutical glaze* (or, *confectioner's glaze*). Because of its acidic properties (resisting stomach acids), shellac-coated pills may be used for a timed enteric or colonic release.[19] Shellac is used as a 'wax' coating on citrus fruit to prolong its shelf/storage life. It is also used to replace the natural wax of the apple, which is removed during the cleaning process.[20] When used for this purpose, it has the food additive E number E904.

Shellac coating applied with either a standard or modified Huon-Stuehrer nozzle, can be economically micro-sprayed onto various smooth sweets, such as chocolate coated peanuts. Irregularities on the surface of the product being sprayed typically result in the formation of unsightly aggregates ("lac-aggs") which precludes the use of this technique on foods such as walnuts or raisins (however, chocolate-coated raisins being smooth surfaced, are able to be sprayed successfully using a modified Huon-Stuehrer nozzle).

Shellac is an odour and stain blocker and so is often used as the base of "solves all problems" primers. Although its durability against abrasives and many common solvents is not very good, shellac provides an excellent barrier against water vapour penetration. Shellac-based primers are an effective sealant to control odours associated with fire damage.

Shellac has traditionally been used as a dye for cotton and, especially, silk cloth in Thailand, particularly in the north-eastern region.[21] It yields a range of warm colours from pale yellow through to dark orange-reds and dark ochre.[22] Naturally dyed silk cloth, including that using shellac, is widely available in the rural northeast, especially in Ban Khwao District, Chaiyaphum province. The Thai name for the insect and the substance is "khrang" (Thai: ครั่ง).

Wood finish

Wood finishing is one of the most traditional and still popular uses of Shellac mixed with solvents or alcohol. This dissolved Shellac liquid, applied to a piece of wood, is an evaporative finish: the alcohol of the shellac mixture evaporates leaving behind a protective film.[23]

Shellac as wood finish is natural and non-toxic in its pure form. A finish made of Shellac is UV-resistant. For water-resistance and durability, it does not keep up with synthetic finishing products.[24]

Because it is compatible with most other finishes, shellac is also used as a barrier or primer coat on wood to prevent the bleeding of resin or pigments into the final finish, or to prevent wood stain from blotching.[25]

Other

Shellac is used:

- in the tying of artificial flies for trout and salmon where the shellac was used to seal all trimmed materials at the head of the fly.
- in combination with wax for preserving and imparting a shine to citrus fruits, such as lemons.

- in dental technology, where it is occasionally used in the production of custom impression trays and (partial) denture production.
- as a binder in India ink.
- for cycling as a protective and decorative coating for bicycle handlebar tape,[26] and as a hard-drying adhesive for tubular cycle tyres, particularly for track racing.[27]
- for re-attaching ink sacs when restoring vintage fountain pens, the orange variety preferably.
- for fixing pads to the key-cups of woodwind instruments.
- for Luthier applications, to bind wood fibres down and prevent tear out on the soft spruce soundboards.
- to stiffen and impart water-resistance to felt hats, for wood finishing[28] and as a constituent of *gossamer* (or *goss* for short), a cheesecloth fabric coated in shellac and ammonia solution used in the shell of traditional silk top and riding hats.
- for mounting insects, in the form of a gel adhesive mixture composed of 75% ethyl alcohol.[29]
- as a binder in the fabrication of abrasive wheels,[30] imparting flexibility and smoothness not found in vitrified (ceramic bond) wheels. 'Elastic' bonded wheels typically contain plaster of paris, yielding a stronger bond when mixed with shellac; the mixture of dry plaster powder, abrasive (e.g. corundum/aluminium oxide Al_2O_3), and shellac are heated and the mixture pressed in a mould.
- in fireworks pyrotechnic compositions as a low-temperature fuel, where it allows the creation of pure 'greens' and 'blues'- colours difficult to achieve with other fuel mixes.
- in watchmaking, due to its low melting temperature (about 80-100 °C), shellac is used in most mechanical movements to adjust and adhere pallet stones to the pallet fork and secure the roller jewel to the roller table of the balance wheel. Also for securing small parts to a 'wax chuck' (faceplate) in a watchmakers' lathe.
- in the early twentieth century, it was used to protect some military rifle stocks.[31]
- in Jelly Belly jelly beans, in combination with beeswax to give them their final buff and polish.[32]
- in modern traditional archery, shellac is one of the hot-melt glue/resin products used to attach arrowheads to wooden or bamboo arrow shafts.
- Sanding sealer, is a solution of shellac dissolved in alcohol widely sold to seal sanded surfaces, typically wooden surfaces before a final coat of a more durable finish. Similar to French Polish but more dilute.
- as a topcoat in nail polish (although not all nail polish sold as "shellac" contains shellac, and some nail polish not labelled in this way does)

Gallery



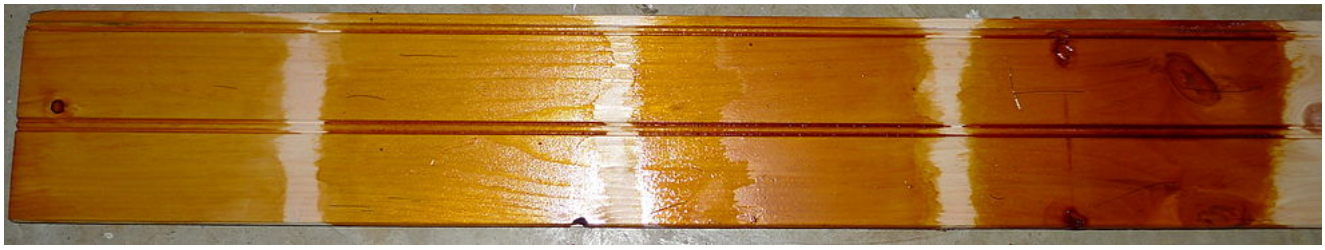
Blonde shellac flakes



Dewaxed Bona (L) and Waxy #1 Orange (R) shellac flakes. The latter—orange shellac—is the traditional shellac used for decades to finish wooden wall paneling, kitchen cabinets and tool handles.



Closeup of Waxy #1 Orange (L) and Dewaxed Bona (R) shellac flakes. The former—orange shellac—is the traditional shellac used for decades to finish wooden wall paneling and kitchen cabinets.



"Quick and dirty" example of a pine board coated with 1-5 coats of Dewaxed Dark shellac (a darker version of traditional orange shellac)

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Horticulture/Biological Pest Control

Biological control of pests and diseases is a method of controlling pests and diseases in agriculture that relies on natural predation rather than introduced chemicals.



Predatory Polistes wasp looking for bollworms or other caterpillars on a cotton plant

Overview



Diagram illustrating the natural enemies of cabbage pests

A key belief of the organic gardener is that biodiversity furthers health. The more variety a landscape has, the more sustainable it is. The organic gardener therefore works to create a system where the insects that are sometimes called pests and the pathogens that cause diseases are not eradicated, but instead are kept at manageable levels by a complex system of checks and balances within a living and vibrant ecosystem. Contrary to more 'conventional' gardening practices which often use chemical methods to kill both useful and harmful garden life forms indiscriminately, this is a holistic approach that seeks to develop an understanding of the webs of interaction between the myriad of organisms that constitute the garden fauna and flora. The organic gardener will often hold the view for example that the eradication of the creatures that are often described as pests is not only not possible, but also undesirable, for without them the beneficial predatory and parasitic insects which depend upon them as food or hosts would not be able to survive.

In a healthy natural woodland where there is little direct human intervention, pest and disease organisms will always be present, but, unless there is a drastic environmental change, will normally kept in a state of equilibrium where they are not able to get out of hand to a level which is detrimental to the overall woodland community. This is the model for which the sensitive organic gardener will strive, but at the same time it is wise to recognise that there will often be some degree of intervention needed to manipulate the natural checks and balances to the gardener's favour, particularly if growing plants for food or ornament which would not normally occur in natural situations. Therefore biological control is about developing a range of techniques that use living organisms to maintain the beneficial equilibria in garden landscapes without causing adverse effects to humans or the wider environment. Of course, introducing exotic insects into any ecosystem entails taking risks of moving further from the intended equilibrium through unexpected interactions.

An important part of the biological gardening approach is to become familiar with the various life forms that inhabit the garden, predators as well as pests, and also their life cycles, patterns of feeding and the habitats that they prefer.

Insects have devised many ways to eat other insects. Predators will directly attack and devour their prey, whilst parasitoids will deposit an egg within another insects body, from which a larva will emerge which will devour the host's innards.

Examples of predators

ladybugs, and in particular their larvae which are active between May and July, are voracious predators of aphids, and will also consume mites, scale insects and small caterpillars. The ladybird is a very familiar beetle with red and black markings, whilst its larvae are initially small and spidery, growing up to 17 mm long. It has a tapering segmented grey/black body with orange/yellow markings nettles in the garden and by leaving hollow stems and some plant debris over-winter so that they can hibernate over winter.



Ladybird larva eating wooly apple aphids

Hoverflies are another very welcome garden predator. Resembling slightly darker bees or wasps, they have characteristic hovering, darting flight patterns. There are over 100 species of hoverfly whose larvae principally feed upon greenfly, one larva devouring up to fifty a day, or 1000 in its lifetime. They also eat fruit tree spider mites and small caterpillars. Adults feed on nectar and pollen, which they require for egg production. Eggs are minute (1 mm), pale yellow white and laid singly near greenfly colonies. Larvae are 8–17 mm long, disguised to resemble bird droppings, they are legless and have no distinct head. Semi-transparent in a range of colours from green, white, brown and black.



Lacewings are available from biocontrol dealers.

Hoverflies can be encouraged by growing attractant flowers such as the poached egg plant *(Limnanthes douglasii)*, marigolds or phacelia throughout the growing season.

Dragonflies are important predators of mosquitoes, both in the water, where the dragonfly nyads eat mosquito larvae, and in the air, where adult dragonflies capture and eat adult mosquitoes. Community-wide mosquito control programs that spray adult mosquitoes also kill dragonflies, thus removing an important biocontrol agent, and can actually increase mosquito populations in the long term.

Other useful garden predators include lacewings, anthrocorid bugs, rove and ground beetles, aphid midge, centipedes, predatory mites, as well as megafauna such as frogs, toads, hedgehogs, slow-worms and birds. Cats and rat terriers kill field mice, rats, June bugs, and birds. Dogs chase away many types of pest animals. Dachshunds are bred specifically to fit inside tunnels underground to kill gophers and rabbits.

Parasitic wasps

A diverse range of wasps lay their eggs on or in the body of an insect host, which is then used as a food for developing wasps. Parasitic wasps take much longer than predators to consume their victims, for if the larvae were to eat too fast they would run out of food before they became adults. Such parasites are very useful in the organic garden, for they are very efficient hunters, always at work searching for pest invaders. As adults they require high energy fuel as they fly from place to place, and feed upon nectar, pollen and sap, therefore planting plenty of flowering plants, particularly buckwheat, umbellifers and composites will encourage their presence.

Three of the most important groups are;

- Ichneumon Flies: (5–10 mm). Prey mainly on caterpillars.
- Braconid Wasps: Tiny wasps (up to 5 mm) attack caterpillars and a wide range of other insects including greenfly. A common parasite of the cabbage white caterpillar- seen as clusters of sulphur yellow cocoons bursting from collapsed caterpillar skin.
- Chalcid Wasps: Among the smallest of insects (<3 mm). Parasitize eggs/larvae of Aphids, Horticulture/Whiteflies, cabbage caterpillars, Scale Insects and strawberry tortrix moth.

Plants to regulate insect pests

Choosing a diverse range of plants for the garden can help to regulate pests in a variety of ways, including;

- Masking the crop plants from pests, depending on the proximity of the companion or intercrop.
- Producing olfactory inhibitors, odors that confuse and deter pests.

Acting as trap plants by providing an alluring food that entices pests away from crops.

- Serving as nursery plants, providing breeding grounds for beneficial insects.
- Providing an alternative habitat, usually in a form of a shelterbelt, hedgerow, or w:beetle bank where beneficial insects can live and reproduce. Nectar-rich plants that bloom for long periods are especially good, as many beneficials are nectivorous during the adult stage, but parasitic or predatory as larvae. A good example of this is the soldier beetle which is frequently found on flowers as an adult, but whose larvae eat aphids, caterpillars, grasshopper eggs, and other beetles.

The following are plants often used in vegetable gardens to deter insects [1]

- **Basil** — Repels flies and mosquitoes.
- **Catnip** — Deters flea beetle.
- **Garlic** — Deters Japanese beetle.
- **Horseradish** — Deters potato bugs.
- **Marigold** — The workhorse of pest deterrents. Discourages Mexian bean beetles, nematodes and others.
- **Mint** — Deters white cabbage moth.
- **Nasturium** — Deters aphids, squash bugs and striped pumpkin beetles.
- **Pot Marigold** — Deters asparagus beetles, tomato worm, and general garden pests.
- **Peppermint** — Repels the white cabbage butterfly.
- **Rosemary** — Deters cabbage moth, bean beetles and carrot fly.
- **Sage** — Deters cabbage moth and carrot fly.
- **Southern Wood** — Deters cabbage moth.
- **Summer Savory** — Deters bean beetles.
- **Tansy** — Deters flying insects, Japanese beetles, striped cucumber beetles, squash bugs and ants.
- **Thyme** — Deters cabbage worm.
- **Wormwood** — Deters animals from garden.

Directly introducing biological controls

Most of the biological controls listed above depend on providing incentives in order to 'naturally' attract beneficial insects to the garden. However there are occasions when biological controls can be directly introduced. Common biocontrol agents include parasitoids, predators, pathogens or weed feeders. This is particularly appropriate in situations such as the greenhouse, a largely artificial environment, and are usually purchased by mail order.

Some biocontrol agents that can be introduced include;

- *Encarsia formosa*. This is a small predatory chaclid wasp which is parasitical on whitefly, a sap-feeding insect which can cause wilting and black sooty moulds. It is most effective when dealing with low level infestations, giving protection over a long period of time. The wasp lays its eggs in young whitefly 'scales', turning them black as the parasite larvae pupates. It should be introduced as soon as possible after the first adult whitefly are seen. Should be used in conjunction with insecticidal soap.
- Red spider mite, another pest found in the greenhouse, can be controlled with the predatory mite *Phytoseilus persimilis*. This is slightly larger than its prey and has an orange body. It develops from egg to adult twice as fast as the red spider mite and once established quickly overcomes infestation.

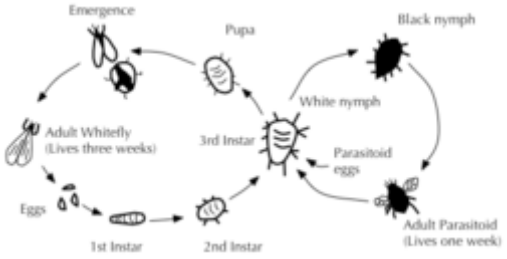


Diagram illustrating the life cycles of Greenhouse whitefly and its parasitoid wasp Encarsia formosa

- A fairly recent development in the control of slugs is the introduction of 'Nemaslug', a microscopic nematode (*Phasmarhabditis hermaphrodita*) which will seek out and Parasitize slugs, reproducing inside them and killing them. The nematode is applied by watering onto moist soil, and gives protection for up to six weeks in optimum conditions, though is mainly effective with small and young slugs under the soil surface.
- A bacterial biological control which can be introduced in order to control butterfly caterpillars is *Bacillus thuringiensis*. This available in sachets of dried spores which are mixed with water and sprayed onto vulnerable plants such as brassicas and fruit trees. The bacterial disease will kill the caterpillars, but leave other insects unharmed. There are strains of *Bt* that are effective against other insect larvae. *Bt israelensis* is effective against mosquito larvae and some midges.
- A biological control being developed for use in the treatment of plant disease is the fungus *Trichoderma viride*. Trichoderma species are free - living fungi that are very common in root ecosystems. This has been used against Dutch Elm disease, and to treat the spread of fungal and bacterial growth on tree wounds. It may also have potential as a means of combating silver leafroo disease.

Economics of biological pest control

Biological control proves to be very successful economically, and even when the method has been less successful, it still produces a benefit-to-cost ratio of 11:1. One study has estimated that a successful biocontrol program returns £32 in benefits for each £1 invested in developing and implementing the program, i.e., a 32:1 benefit-to-cost ratio. The same study had shown that an average chemical pesticide program only returned profits in the ratio of 2.5:1.

See also

- w:Insectary plants

References

1. "Notes on Natural Pest Control for an Organic Garden - DigGood.com". http://www.didgood.com/health/naturalpestcontrol.html.

External links

- Biological Control: A Guide to Natural Enemies in North America (http://www.nysaes.cornell.edu/ent/biocontrol/)
- Beyond Pesticides (http://www.beyondpesticides.org) - Provides information on pesticides and alternatives to their use
- GreenMethods.com (http://www.greenmethods.com) - Extensive biocontrol and IPM information resource

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Biological pest control

Biological control or **biocontrol** is a method of controlling pests such as insects, mites, weeds and plant diseases using other organisms.[1] It relies on predation, parasitism, herbivory, or other natural mechanisms, but typically also involves an active human management role. It can be an important component of integrated pest management (IPM) programs.

There are three basic strategies for biological pest control: classical (importation), where a natural enemy of a pest is introduced in the hope of achieving control; inductive (augmentation), in which a large population of natural enemies are administered for quick pest control; and inoculative (conservation), in which measures are taken to maintain natural enemies through regular reestablishment.[2]

Natural enemies of insect pests, also known as biological control agents, include predators, parasitoids, pathogens, and competitors. Biological control agents of plant diseases are most often referred to as antagonists. Biological control agents of weeds include seed predators, herbivores and plant pathogens.

Biological control can have side-effects on biodiversity through attacks on non-target species by any of the same mechanisms, especially when a species is introduced without thorough understanding of the possible consequences.



Syrphus hoverfly larva (below) feed on aphids (above), making them natural biological control agents.



A parasitoid wasp (*Cotesia congregata*) adult with pupal cocoons on its host, a tobacco hornworm (*Manduca sexta*, green background), an example of a hymenopteran biological control agent

Contents

History

Types of biological pest control
- Importation
- Augmentation
- Conservation

Biological control agents
- Predators
- Parasitoids
- Pathogens
 - Bacteria
 - Fungi
 - Viruses
 - Oomycota
- Competitors
- Combined use of parasitoids and pathogens

Difficulties
- Side effects

Grower education
See also
References
Further reading
External links

History

The term "biological control" was first used by Harry Scott Smith at the 1919 meeting of the Pacific Slope Branch of the American Association of Economic Entomologists, in Riverside, California.[3] It was brought into more widespread use by the entomologist Paul H. DeBach (1914–1993) who worked on citrus crop pests throughout his life.[4][5] However, the practice has previously been used for centuries. The first report of the use of an insect species to control an insect pest comes from "Nanfang Caomu Zhuang" (南方草木狀 *Plants of the Southern Regions*) (c. 304 AD), attributed to Western Jin dynasty botanist *Ji Han* (嵇含, 263–307), in which it is mentioned that "*Jiaozhi people sell ants and their nests attached to twigs looking like thin cotton envelopes, the reddish-yellow ant being larger than normal. Without such ants, southern citrus fruits will be severely insect-damaged*".[6] The ants used are known as *huang gan* (*huang* = yellow, *gan* = citrus) ants (*Oecophylla smaragdina*). The practice was later reported by Ling Biao Lu Yi (late Tang Dynasty or Early Five Dynasties), in *Ji Le Pian* by *Zhuang Jisu* (Southern Song Dynasty), in the *Book of Tree Planting* by Yu Zhen Mu (Ming Dynasty), in the book *Guangdong Xing Yu* (17th century), *Lingnan* by Wu Zhen Fang (Qing Dynasty), in *Nanyue Miscellanies* by Li Diao Yuan, and others.[6]

Biological control techniques as we know them today started to emerge in the 1870s. During this decade, in the US, the Missouri State Entomologist C. V. Riley and the Illinois State Entomologist W. LeBaron began within-state redistribution of parasitoids to control crop pests. The first international shipment of an insect as biological control agent was made by Charles V. Riley in 1873, shipping to France the predatory mites *Tyroglyphus phylloxera* to help fight the grapevine phylloxera (*Daktulosphaira vitifoliae*) that was destroying grapevines in France. The United States Department of Agriculture (USDA) initiated research in classical biological control following the establishment of the Division of Entomology in 1881, with C. V. Riley as Chief. The first importation of a parasitoidal wasp into the United States was that of the braconid *Cotesia glomerata* in 1883–1884, imported from Europe to control the invasive cabbage white butterfly, *Pieris rapae*. In 1888–1889 the vedalia beetle, *Rodolia cardinalis*, a lady beetle, was introduced from Australia to California to control the cottony cushion scale, *Icerya purchasi*. This had become a major problem for the newly developed citrus industry in California, but by the end of 1889 the cottony cushion scale population had already declined. This great success led to further introductions of beneficial insects into the US.[7][8]

In 1905 the USDA initiated its first large-scale biological control program, sending entomologists to Europe and Japan to look for natural enemies of the gypsy moth, *Lymantria dispar dispar*, and brown-tail moth, *Euproctis chrysorrhoea*, invasive pests of trees and shrubs. As a result, nine parasitoids (solitary wasps) of gypsy moth, seven of brown-tail moth, and two predators of both moths became established in the US. Although the gypsy moth was not fully controlled by these natural enemies, the frequency, duration, and severity of its outbreaks were reduced and the program was regarded as successful. This program also led to the development of many concepts, principles, and procedures for the implementation of biological control programs.[7][8][9]

Prickly pear cacti were introduced into Queensland, Australia as ornamental plants, starting in 1788. They quickly spread to cover over 25 million hectares of Australia by 1920, increasing by 1 million hectares per year. Digging, burning and crushing all proved ineffective. Two control agents were introduced to help control the spread of the plant, the cactus moth *Cactoblastis cactorum*, and the scale insect *Dactylopius*. Between 1926 and 1931, tens of millions of cactus moth eggs were distributed around Queensland with great success, and by 1932, most areas of prickly pear had been destroyed.[10]

The first reported case of a classical biological control attempt in Canada involves the parasitoidal wasp *Trichogramma minutum*. Individuals were caught in New York State and released in Ontario gardens in 1882 by William Saunders, trained chemist and first Director of the Dominion Experimental Farms, for controlling the invasive currantworm *Nematus ribesii*. Between 1884 and

1908, the first Dominion Entomologist, James Fletcher, continued introductions of other parasitoids and pathogens for the control of pests in Canada.[11]



Cactoblastis cactorum larvae feeding on *Opuntia* prickly pear cacti

Types of biological pest control

There are three basic biological pest control strategies: importation (classical biological control), augmentation and conservation.[12]

Importation



Rodolia cardinalis, the vedalia beetle, was imported from Australia to California in the 19th century, successfully controlling cottony cushion scale.

Importation or classical biological control involves the introduction of a pest's natural enemies to a new locale where they do not occur naturally. Early instances were often unofficial and not based on research, and some introduced species became serious pests themselves.[13]

To be most effective at controlling a pest, a biological control agent requires a colonizing ability which allows it to keep pace with changes to the habitat in space and time. Control is greatest if the agent has temporal persistence, so that it can maintain its population even in the temporary absence of the target species, and if it is an opportunistic forager, enabling it to rapidly exploit a pest population.[14]

Joseph Needham noted a Chinese text dating from 304 AD, *Records of the Plants and Trees of the Southern Regions*, by Hsi Han, which describes mandarin oranges protected by large reddish-yellow citrus ants which attack and kill insect pests of the orange trees. The citrus ant (*Oecophylla smaragdina*)[15] was rediscovered in the 20th century, and since 1958 has been used in China to protect orange groves.[16]

One of the earliest successes in the west was in controlling *Icerya purchasi* (cottony cushion scale) in Australia, using a predatory insect *Rodolia cardinalis* (the vedalia beetle). This success was repeated in California using the beetle and a parasitoidal fly, *Cryptochaetum iceryae*.[17] Other successful cases include the control of *Antonina graminis* in Texas by *Neodusmetia sangwani* in the 1960s.[18]

Damage from *Hypera postica*, the alfalfa weevil, a serious introduced pest of forage, was substantially reduced by the introduction of natural enemies. 20 years after their introduction the population of weevils in the alfalfa area treated for alfalfa weevil in the Northeastern United States remained 75 percent down.[19]

Alligator weed was introduced to the United States from South America. It takes root in shallow water, interfering with navigation, irrigation, and flood control. The alligator weed flea beetle and two other biological controls were released in Florida, greatly reducing the amount of land covered by the plant.[20] Another aquatic weed, the giant salvinia (*Salvinia molesta*) is a serious pest, covering waterways, reducing water flow and harming native species. Control with the salvinia weevil (*Cyrtobagous salviniae*) and the salvinia stem-borer moth (*Samea multiplicalis)* is effective in warm climates,[21][22] and in Zimbabwe, a 99% control of the weed was obtained over a two-year period.[23]

Small commercially reared parasitoidal wasps,[12] *Trichogramma ostriniae*, provide limited and erratic control of the European corn borer (*Ostrinia nubilalis*), a serious pest. Careful formulations of the bacterium *Bacillus thuringiensis* are more effective.[24]

The population of *Levuana iridescens*, the Levuana moth, a serious coconut pest in Fiji, was brought under control by a classical biological control program in the 1920s.[25]



The invasive species *Alternanthera philoxeroides* (alligator weed) was controlled in Florida (U.S.) by introducing alligator weed flea beetle.

Augmentation

Augmentation involves the supplemental release of natural enemies that occur in a particular area, boosting the naturally occurring populations there. In inoculative release, small numbers of the control agents are released at intervals to allow them to reproduce, in the hope of setting up longer-term control, and thus keeping the pest down to a low level, constituting prevention rather than cure. In inundative release, in contrast, large numbers are released in the hope of rapidly reducing a damaging pest population, correcting a problem that has already arisen. Augmentation can be effective, but is not guaranteed to work, and depends on the precise details of the interactions between each pest and control agent.[26]



Hippodamia convergens, the convergent lady beetle, is commonly sold for biological control of aphids.

An example of inoculative release occurs in the horticultural production of several crops in greenhouses. Periodic releases of the parasitoidal wasp, *Encarsia formosa*, are used to control greenhouse whitefly,[27] while the predatory mite *Phytoseiulus persimilis* is used for control of the two-spotted spider mite.[28]

The egg parasite *Trichogramma* is frequently released inundatively to control harmful moths. Similarly, *Bacillus thuringiensis* and other microbial insecticides are used in large enough quantities for a rapid effect.[26] Recommended release rates for *Trichogramma* in vegetable or field crops range from 5,000 to 200,000 per acre (1 to 50 per square metre) per week according to the level of pest infestation.[29] Similarly, nematodes that kill insects (that are entomopathogenic) are released at rates of millions and even billions per acre for control of certain soil-dwelling insect pests.[30]

Conservation

The conservation of existing natural enemies in an environment is the third method of biological pest control.[31] Natural enemies are already adapted to the habitat and to the target pest, and their conservation can be simple and cost-effective, as when nectar-producing crop plants are grown in the borders of rice fields. These provide nectar to support parasitoids and predators of planthopper pests and have been demonstrated to be so effective (reducing pest densities by 10- or even 100-fold) that farmers sprayed 70% less insecticides and enjoyed yields boosted by 5%.[32] Predators of aphids were similarly found to be present in tussock grasses by field boundary hedges in England, but they spread too slowly to reach the centres of fields. Control was improved by planting a metre-wide strip of tussock grasses in field centres, enabling aphid predators to overwinter there.[31]

Cropping systems can be modified to favor natural enemies, a practice sometimes referred to as habitat manipulation. Providing a suitable habitat, such as a shelterbelt, hedgerow, or beetle bank where beneficial insects such as parasitoidal wasps can live and reproduce, can help ensure the survival of populations of natural enemies. Things as simple as leaving a layer of fallen leaves or mulch in place provides a suitable food source for worms and provides a shelter for insects, in turn being a food source for such beneficial mammals as hedgehogs and shrews. Compost piles and stacks of wood can provide shelter for invertebrates and small mammals. Long grass and ponds support amphibians. Not removing dead annuals and non-hardy plants in the autumn allows insects to make use of their hollow stems during winter.[33] In California, prune trees are sometimes planted in grape vineyards to provide an improved overwintering habitat or refuge for a key grape pest parasitoid.[34] The providing of artificial shelters in the form of wooden caskets, boxes or flowerpots is also sometimes undertaken, particularly in gardens, to make a cropped area more

attractive to natural enemies. For example, earwigs are natural predators which can be encouraged in gardens by hanging upside-down flowerpots filled with straw or wood wool. Green lacewings can be encouraged by using plastic bottles with an open bottom and a roll of cardboard inside. Birdhouses enable insectivorous birds to nest; the most useful birds can be attracted by choosing an opening just large enough for the desired species.[33]

In cotton production, the replacement of broad-spectrum insecticides with selective control measures such as Bt cotton can create a more favorable environment for natural enemies of cotton pests due to reduced insecticide exposure risk. Such predators or parasitoids can control pests not affected by the Bt protein. Reduced prey quality and abundance associated increased control from Bt cotton can also indirectly decrease natural enemy populations in some cases, but the percentage of pests eaten or parasitized in Bt and non-Bt cotton are often similar.[35]



An inverted flowerpot filled with straw to attract earwigs

Biological control agents

Predators



Predatory lacewings are available from biocontrol dealers.

Predators are mainly free-living species that directly consume a large number of prey during their whole lifetime. Given that many major crop pests are insects, many of the predators used in biological control are insectivorous species. Lady beetles, and in particular their larvae which are active between May and July in the northern hemisphere, are voracious predators of aphids, and also consume mites, scale insects and small caterpillars. The spotted lady beetle (*Coleomegilla maculata*) is also able to feed on the eggs and larvae of the Colorado potato beetle (*Leptinotarsa decemlineata*).[36]

The larvae of many hoverfly species principally feed upon aphids, one larva devouring up to 400 in its lifetime. Their effectiveness in commercial crops has not been studied.[37]

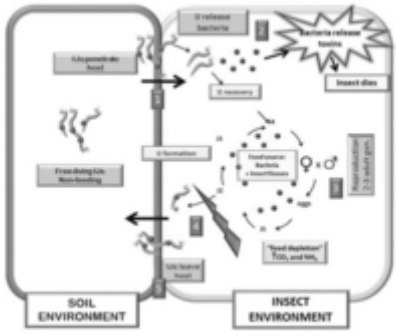


Predatory *Polistes* wasp searching for bollworms or other caterpillars on a cotton plant

Several species of entomopathogenic nematode are important predators of insect and other invertebrate pests.[38][39] Entomopathogenic nematodes form a stress–resistant stage known as the infective juvenile. These spread in the soil and infect suitable insect hosts. Upon entering the insect they move to the hemolymph where they recover from their stagnated state of development and release their bacterial symbionts. The bacterial symbionts reproduce and release toxins, which then kill the host insect.[39][40] *Phasmarhabditis hermaphrodita* is a microscopic nematode that kills slugs. Its complex life cycle includes a free-living, infective stage in the soil where it becomes associated with a pathogenic bacteria such as *Moraxella osloensis*. The nematode enters the slug through the posterior mantle region, thereafter feeding and reproducing inside, but it is the bacteria that kill the slug. The nematode is available commercially in Europe and

is applied by watering onto moist soil.[41] Entomopathogenic nematodes have a limited shelf life because of their limited resistance to high temperature and dry conditions.[40] The type of soil they are applied to may also limit their effectiveness.[39]

Species used to control spider mites include the predatory mites *Phytoseiulus persimilis*,[42] *Neoseilus californicus*,[43] and *Amblyseius cucumeris*, the predatory midge *Feltiella acarisuga*,[43] and a ladybird *Stethorus punctillum*.[43] The bug *Orius insidiosus* has been successfully used against the two-spotted spider mite and the western flower thrips (*Frankliniella occidentalis*).[44]



Generalized life cycle of entomopathogenic nematodes and their bacterial symbionts.

Predators including *Cactoblastis cactorum* (mentioned above) can also be used to destroy invasive plant species. As another example, the poison hemlock moth (*Agonopterix alstroemeriana)* can be used to control poison hemlock (*Conium maculatum*). During its larval stage, the moth strictly consumes its host plant, poison hemlock, and can exist at hundreds of larvae per individual host plant, destroying large swathes of the hemlock.[45]

For rodent pests, cats are effective biological control when used in conjunction with reduction of "harborage"/hiding locations.[47][48][49] While cats are effective at preventing rodent "population explosions", they are not effective for eliminating pre-existing severe infestations.[49] Barn owls are also sometimes used as biological rodent control.[50] Although there are no quantitative studies of the effectiveness of barn owls for this purpose,[51] they are known rodent predators that can be used in addition to or instead of cats;[52][53] they can be encouraged into an area with nest boxes.[54][55]


The parasitoid wasp *Aleiodes indiscretus* parasitizing a gypsy moth caterpillar, a serious pest of forestry[46]

Parasitoids

Parasitoids lay their eggs on or in the body of an insect host, which is then used as a food for developing larvae. The host is ultimately killed. Most insect parasitoids are wasps or flies, and many have a very narrow host range. The most important groups are the ichneumonid wasps, which mainly use caterpillars as hosts; braconid wasps, which attack caterpillars and a wide range of other insects including aphids; chalcid wasps, which parasitize eggs and larvae of many insect species; and tachinid flies, which parasitize a wide range of insects including caterpillars, beetle adults and larvae, and true bugs.[56] Parasitoids are most effective at reducing pest populations when their host organisms have limited refuges to hide from them.[57]

Parasitoids are among the most widely used biological control agents. Commercially, there are two types of rearing systems: short-term daily output with high production of parasitoids per day, and long-term, low daily output systems.[58] In most instances, production will need to be matched with the appropriate release dates when susceptible host species at a suitable phase of development will be available.[59] Larger production facilities produce on a yearlong basis, whereas some facilities produce only seasonally. Rearing facilities are usually a significant distance from where the agents are to be used in the field, and transporting the parasitoids from the point of production to the point of use can pose problems.[60] Shipping conditions can be too hot, and even vibrations from planes or trucks can adversely affect parasitoids.[58]

Encarsia formosa is a small predatory chalcid wasp which is a parasitoid of whitefly, a sap-feeding insect which can cause wilting and black sooty moulds in glasshouse vegetable and ornamental crops. It is most effective when dealing with low level infestations, giving protection over a long period of time. The wasp lays its eggs in young whitefly 'scales', turning them black as

the parasite larvae pupate.[27] *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae) has been introduced to control the glassy-winged sharpshooter *Homalodisca vitripennis* (Hemiptera: Cicadellidae) in French Polynesia and has successfully controlled ~95% of the pest density.[61]

The eastern spruce budworm is an example of a destructive insect in fir and spruce forests. Birds are a natural form of biological control, but the *Trichogramma minutum*, a species of parasitic wasp, has been investigated as an alternative to more controversial chemical controls.[62]

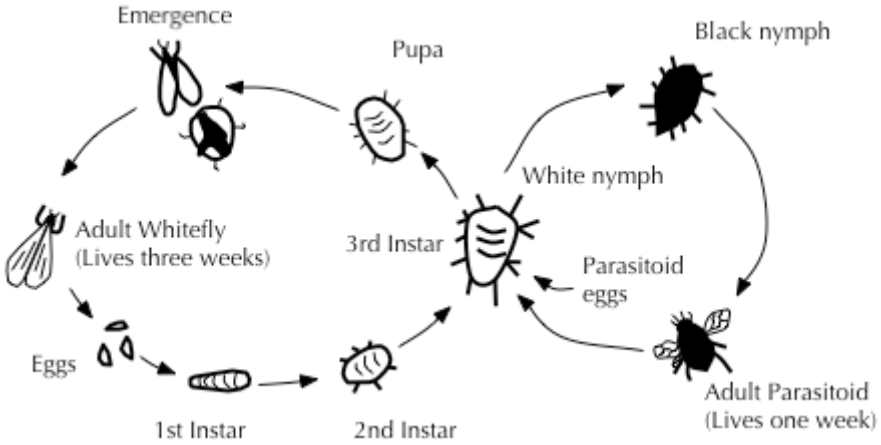
There are a number of recent studies pursuing sustainable methods for controlling urban cockroaches using parasitic wasps.[63][64] Since most cockroaches remain in the sewer system and sheltered areas which are inaccessible to insecticides, employing active-hunter wasps is a strategy to try and reduce their populations.



Encarsia formosa, widely used in greenhouse horticulture, was one of the first biological control agents developed.

Pathogens

Pathogenic micro-organisms include bacteria, fungi, and viruses. They kill or debilitate their host and are relatively host-specific. Various microbial insect diseases occur naturally, but may also be used as biological pesticides.[65] When naturally occurring, these outbreaks are density-dependent in that they generally only occur as insect populations become denser.[66]



Life cycles of greenhouse whitefly and its parasitoid wasp *Encarsia formosa*

Bacteria

Bacteria used for biological control infect insects via their digestive tracts, so they offer only limited options for controlling insects with sucking mouth parts such as aphids and scale insects.[67] *Bacillus thuringiensis*, a soil-dwelling bacterium, is the most widely applied species of bacteria used for biological control, with at least four sub-species used against Lepidopteran (moth, butterfly), Coleopteran (beetle) and Dipteran (true fly) insect pests. The bacterium is available to organic farmers in sachets of dried spores which are mixed with water and sprayed onto vulnerable plants such as brassicas and fruit trees.[68][69] Genes from *B. thuringiensis* have also been incorporated into transgenic crops, making the plants express some of the bacterium's toxins, which are proteins. These confer resistance to insect pests and thus reduce the necessity for pesticide use.[70] If pests develop resistance to the toxins in these crops, *B. thuringiensis* will become useless in organic farming also.[71][69] The bacterium *Paenibacillus popilliae* which causes milky spore disease has been found useful in the control of Japanese beetle, killing the larvae. It is very specific to its host species and is harmless to vertebrates and other invertebrates.[72]

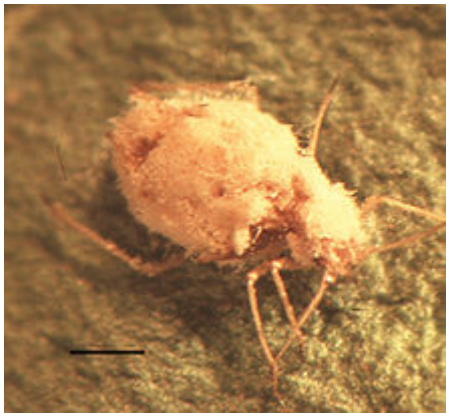
Fungi

Entomopathogenic fungi, which cause disease in insects, include at least 14 species that attack aphids.[73] *Beauveria bassiana* is mass-produced and used to manage a wide variety of insect pests including whiteflies, thrips, aphids and weevils.[74] *Lecanicillium* spp. are deployed against white flies, thrips and aphids. *Metarhizium* spp. are used against pests including beetles, locusts and other grasshoppers, Hemiptera, and spider mites. *Paecilomyces fumosoroseus* is effective against white flies, thrips

and aphids; *Purpureocillium lilacinus* is used against root-knot nematodes, and 89 *Trichoderma* species against certain plant pathogens. *Trichoderma viride* has been used against Dutch elm disease, and has shown some effect in suppressing silver leaf, a disease of stone fruits caused by the pathogenic fungus *Chondrostereum purpureum*.[75]

The fungi *Cordyceps* and *Metacordyceps* are deployed against a wide spectrum of arthropods.[76] *Entomophaga* is effective against pests such as the green peach aphid.[77]

Several members of Chytridiomycota and Blastocladiomycota have been explored as agents of biological control.[78][79] From Chytridiomycota, *Synchytrium solstitiale* is being considered as a control agent of the yellow star thistle (*Centaurea solstitialis*) in the United States.[80]



Green peach aphid, a pest in its own right and a vector of plant viruses, killed by the fungus *Pandora neoaphidis* (Zygomycota: Entomophthorales) Scale bar = 0.3 mm.

Viruses

Baculoviruses are specific to individual insect host species and have been shown to be useful in biological pest control. For example, the Lymantria dispar multicapsid nuclear polyhedrosis virus has been used to spray large areas of forest in North America where larvae of the gypsy moth are causing serious defoliation. The moth larvae are killed by the virus they have eaten and die, the disintegrating cadavers leaving virus particles on the foliage to infect other larvae.[81]

A mammalian virus, the rabbit haemorrhagic disease virus was introduced to Australia to attempt to control the European rabbit populations there.[82] It escaped from quarantine and spread across the country, killing large numbers of rabbits. Very young animals survived, passing immunity to their offspring in due course and eventually producing a virus-resistant population.[83] Introduction into New Zealand in the 1990s was similarly successful at first, but a decade later, immunity had developed and populations had returned to pre-RHD levels.[84]

Oomycota

Lagenidium giganteum is a water-borne mold that parasitizes the larval stage of mosquitoes. When applied to water, the motile spores avoid unsuitable host species and search out suitable mosquito larval hosts. This mold has the advantages of a dormant phase, resistant to desiccation, with slow-release characteristics over several years. Unfortunately, it is susceptible to many chemicals used in mosquito abatement programmes.[85]

Competitors

The legume vine *Mucuna pruriens* is used in the countries of Benin and Vietnam as a biological control for problematic *Imperata cylindrica* grass: the vine is extremely vigorous and suppresses neighbouring plants by out-competing them for space and light. *Mucuna pruriens* is said not to be invasive outside its cultivated area.[86] *Desmodium uncinatum* can be used in push-pull farming to stop the parasitic plant, witchweed (*Striga*).[87]

The Australian bush fly, *Musca vetustissima*, is a major nuisance pest in Australia, but native decomposers found in Australia are not adapted to feeding on cow dung, which is where bush flies breed. Therefore, the Australian Dung Beetle Project (1965–1985), led by George Bornemissza of the Commonwealth Scientific and Industrial Research Organisation, released forty-nine species of dung beetle, to reduce the amount of dung and therefore also the potential breeding sites of the fly.[88]

Combined use of parasitoids and pathogens

In cases of massive and severe infection of invasive pests, techniques of pest control are often used in combination. An example is the emerald ash borer, *Agrilus planipennis*, an invasive beetle from China, which has destroyed tens of millions of ash trees in its introduced range in North America. As part of the campaign against it, from 2003 American scientists and the Chinese Academy of Forestry searched for its natural enemies in the wild, leading to the discovery of several parasitoid wasps, namely *Tetrastichus planipennisi*, a gregarious larval endoparasitoid, *Oobius agrili*, a solitary, parthenogenic egg parasitoid, and *Spathius agrili*, a gregarious larval ectoparasitoid. These have been introduced and released into the United States of America as a possible biological control of the emerald ash borer. Initial results for *Tetrastichus planipennisi* have shown promise, and it is now being released along with *Beauveria bassiana*, a fungal pathogen with known insecticidal properties.[89][90][91]

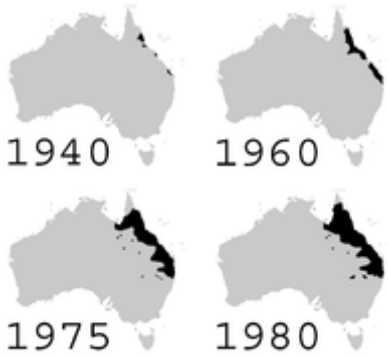
Difficulties

Many of the most important pests are exotic, invasive species that severely impact agriculture, horticulture, forestry and urban environments. They tend to arrive without their co-evolved parasites, pathogens and predators, and by escaping from these, populations may soar. Importing the natural enemies of these pests may seem a logical move but this may have unintended consequences; regulations may be ineffective and there may be unanticipated effects on biodiversity, and the adoption of the techniques may prove challenging because of a lack of knowledge among farmers and growers.[92]

Side effects

Biological control can affect biodiversity[14] through predation, parasitism, pathogenicity, competition, or other attacks on non-target species.[93] An introduced control does not always target only the intended pest species; it can also target native species.[94] In Hawaii during the 1940s parasitic wasps were introduced to control a lepidopteran pest and the wasps are still found there today. This may have a negative impact on the native ecosystem; however, host range and impacts need to be studied before declaring their impact on the environment.[95]

Vertebrate animals tend to be generalist feeders, and seldom make good biological control agents; many of the classic cases of "biocontrol gone awry" involve vertebrates. For example, the cane toad (*Rhinella marina*) was intentionally introduced to Australia to control the greyback cane beetle (*Dermolepida albohirtum*),[96] and other pests of sugar cane. 102 toads were obtained from Hawaii and bred in captivity to increase their numbers until they were released into the sugar cane fields of the tropic north in 1935. It was later discovered that the toads could not jump very high and so were unable to eat the cane beetles which stayed on the upper stalks of the cane plants. However, the toad thrived by feeding on other insects and soon spread very rapidly; it took over native amphibian habitat and brought foreign disease to native toads and frogs, dramatically reducing their populations. Also, when it is threatened or handled, the cane toad releases poison from parotoid glands on its shoulders; native Australian species such as goannas, tiger snakes, dingos and northern quolls that attempted to eat the toad were harmed or killed. However, there has been some recent evidence that native predators are adapting, both physiologically and through changing their behaviour, so in the long run, their populations may recover.[97]



Cane toad (introduced into Australia 1935) spread from 1940 to 1980: it was ineffective as a control agent. Its distribution has continued to widen since 1980.

Rhinocyllus conicus, a seed-feeding weevil, was introduced to North America to control exotic musk thistle (*Carduus nutans*) and Canadian thistle (*Cirsium arvense*). However, the weevil also attacks native thistles, harming such species as the endemic Platte thistle (*Cirsium neomexicanum*) by selecting larger plants (which reduced the gene pool), reducing seed production and ultimately threatening the species' survival.[98] Similarly, the weevil *Larinus planus* was also used to try to control the Canadian thistle, but it damaged other thistles as well.[99][100] This included one species classified as threatened.[101]

The small Asian mongoose (*Herpestus javanicus*) was introduced to Hawaii in order to control the rat population. However, the mongoose was diurnal, and the rats emerged at night; the mongoose therefore preyed on the endemic birds of Hawaii, especially their eggs, more often than it ate the rats, and now both rats and mongooses threaten the birds. This introduction was undertaken without understanding the consequences of such an action. No regulations existed at the time, and more careful evaluation should prevent such releases now.[102]

The sturdy and prolific eastern mosquitofish (*Gambusia holbrooki*) is a native of the southeastern United States and was introduced around the world in the 1930s and '40s to feed on mosquito larvae and thus combat malaria. However, it has thrived at the expense of local species, causing a decline of endemic fish and frogs through competition for food resources, as well as through eating their eggs and larvae.[103] In Australia, control of the mosquitofish is the subject of discussion; in 1989 researchers A. H. Arthington and L. L. Lloyd stated that "biological population control is well beyond present capabilities".[104]

Grower education

A potential obstacle to the adoption of biological pest control measures is that growers may prefer to stay with the familiar use of pesticides. However, pesticides have undesired effects, including the development of resistance among pests, and the destruction of natural enemies; these may in turn enable outbreaks of pests of other species than the ones originally targeted, and on crops at a distance from those treated with pesticides.[105] One method of increasing grower adoption of biocontrol methods involves letting them learn by doing, for example showing them simple field experiments, enabling them to observe the live predation of pests, or demonstrations of parasitised pests. In the Philippines, early season sprays against leaf folder caterpillars were common practice, but growers were asked to follow a 'rule of thumb' of not spraying against leaf folders for the first 30 days after transplanting; participation in this resulted in a reduction of insecticide use by 1/3 and a change in grower perception of insecticide use.[106]

See also

- Beneficial insects
- Biological control of gorse in New Zealand
- Biological pesticide
- Chitosan
- Companion planting
- Insectary plants
- International Organization for Biological Control
- Inundative application
- Japanese beetle
- Mating disruption
- Nematophagous fungus
- Organic gardening
- Organic farming
- Pest control
- Permaculture zone 5
- Sterile insect technique
- Sustainable farming
- Sustainable gardening
- Zero Budget Farming

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Ecosystem services

Ecosystem services are the many and varied benefits that humans freely gain from the natural environment and from properly-functioning ecosystems. Such ecosystems include, for example, agroecosystems, forest ecosystems, grassland ecosystems and aquatic ecosystems. These ecosystems functioning properly provides such things like agricultural produce, timber, and aquatic organisms such as fishes and crabs. Collectively, these benefits are becoming known as 'ecosystem services', and are often integral to the provisioning of clean drinking water, the decomposition of wastes, and the natural pollination of crops and other plants.

While scientists and environmentalists have discussed ecosystem services implicitly for decades, the Millennium Ecosystem Assessment (MA) in the early 2000s popularized this concept.[1] There, ecosystem services are grouped into four broad categories: *provisioning*, such as the production of food and water; *regulating*, such as the control of climate and disease; *supporting*, such as nutrient cycles and oxygen production; and *cultural*, such as spiritual and recreational benefits. To help inform decision-makers, many ecosystem services are being assigned economic values.



Honey bee on Avocado crop. Pollination is just one type of ecosystem service.



Upland bog in Wales, forming the official source of the River Severn. Healthy bogs sequester carbon, hold back water thereby reducing flood risk, and supply cleaned water better than degraded habitats do.



Social forestry in Andhra Pradesh, India, providing fuel, soil protection, shade and even well-being to travellers.

Contents

History

Definition

Categorization

- Supporting services
- Provisioning services
- Regulating services
- Cultural services
- Common International Classification of Ecosystem Services (CICES)

Examples

Ecology

- Redundancy hypothesis
- Portfolio effect

Economics

Management and policy

- Ecosystem-based adaptation (EbA)

Estuarine and coastal ecosystem services

- Regulating services
 - Climate regulation
 - Waste treatment and disease regulation
 - Buffer zones
- Provisioning Services

- Marine products
- Fresh water
- Raw materials
- Biochemical and genetic resources
- Cultural services
 - Inspirational
 - Recreation and tourism
 - Science and education
- Supporting services
 - Nutrient cycling
 - Biologically mediated habitats
 - Primary production

Businessworld

Land use change decisions

See also

References

Further reading

External links

History

While the notion of human dependence on Earth's ecosystems reaches to the start of *Homo sapiens*' existence, the term 'natural capital' was first coined by E.F. Schumacher in 1973 in his book *Small is Beautiful* [2]. Recognition of how ecosystems could provide complex services to humankind date back to at least Plato (c. 400 BC) who understood that deforestation could lead to soil erosion and the drying of springs.[3] Modern ideas of ecosystem services probably began when Marsh challenged in 1864 the idea that Earth's natural resources are unbounded by pointing out changes in soil fertility in the Mediterranean.[4] It was not until the late 1940s that three key authors—Henry Fairfield Osborn, Jr,[5] William Vogt,[6] and Aldo Leopold [7]—promoted recognition of human dependence on the environment.

In 1956, Paul Sears drew attention to the critical role of the ecosystem in processing wastes and recycling nutrients.[8] In 1970, Paul Ehrlich and Rosa Weigert called attention to "ecological systems" in their environmental science textbook[9] and "the most subtle and dangerous threat to man's existence... the potential destruction, by man's own activities, of those ecological systems upon which the very existence of the human species depends".

The term "**environmental services**" was introduced in a 1970 report of the *Study of Critical Environmental Problems*,[10] which listed services including insect pollination, fisheries, climate regulation and flood control. In following years, variations of the term were used, but eventually 'ecosystem services' became the standard in scientific literature.[11]

The ecosystem services concept has continued to expand and includes socio-economic and conservation objectives, which are discussed below. A history of the concepts and terminology of ecosystem services as of 1997, can be found in Daily's book "Nature's Services: Societal Dependence on Natural Ecosystems".[3]

While Gretchen Daily's original definition distinguished between ecosystem goods and ecosystem services, Robert Costanza and colleagues' later work and that of the Millennium Ecosystem Assessment lumped all of these together as ecosystem services.[12][13]

Definition

Per the 2006 Millennium Ecosystem Assessment (MA), ecosystem services are "the benefits people obtain from ecosystems". The MA also delineated the four categories of ecosystem services—supporting, provisioning, regulating and cultural—discussed below.

By 2010, there had evolved various working definitions and descriptions of ecosystem services in the literature.[14] To prevent double counting in ecosystem services audits, for instance, The Economics of Ecosystems and Biodiversity (TEEB) replaced "Supporting Services" in the MA with "Habitat Services" and "ecosystem functions", defined as "a subset of the interactions between ecosystem structure and processes that underpin the capacity of an ecosystem to provide goods and services".[15]

Categorization

The Millennium Ecosystem Assessment (MA) report 2005 defines *Ecosystem services* as benefits people obtain from ecosystems and distinguishes four categories of ecosystem services, where the so-called supporting services are regarded as the basis for the services of the other three categories.[1]



Detritivores like this dung beetle help to turn animal wastes into organic material that can be reused by primary producers.

Supporting services

These include services such as nutrient cycling, primary production, soil formation, habitat provision and pollination.[16] These services make it possible for the ecosystems to continue providing services such as food supply, flood regulation, and water purification. Slade et al [17] outline the situation where a greater number of species would maximise more ecosystem services

Provisioning services

- food (including seafood and game), crops, wild foods, and spices
- raw materials (including lumber, skins, fuel wood, organic matter, fodder, and fertilizer)
- genetic resources (including crop improvement genes, and health care)
- water purity
- biogenic minerals
- medicinal resources (including pharmaceuticals, chemical models, and test and assay organisms)
- energy (hydropower, biomass fuels)
- ornamental resources (including fashion, handicraft, jewelry, pets, worship, decoration and souvenirs like furs, feathers, ivory, orchids, butterflies, aquarium fish, shells, etc.)

Regulating services

- Carbon sequestration and climate regulation
- Predation regulates prey populations
- Waste decomposition and detoxification
- Purification of water and air
- pest and disease control

Cultural services

- cultural (including use of nature as motif in books, film, painting, folklore, national symbols, architect, advertising, etc.)
- spiritual and historical (including use of nature for religious or heritage value or natural)
- recreational experiences (including ecotourism, outdoor sports, and recreation)

- science and education (including use of natural systems for school excursions, and scientific discovery)
- Therapeutic (including Ecotherapy, social forestry and animal assisted therapy)

There is discussion as to how the concept of **cultural ecosystem services** can be operationalized. A good review of approaches in landscape aesthetics, cultural heritage, outdoor recreation, and spiritual significance to define and assess cultural values of our environment so that they fit into the ecosystem services approach is given by Daniel et al.[18] who vote for models that explicitly link ecological structures and functions with cultural values and benefits. There also is a fundamental *critique* of the concept of cultural ecosystem services that builds on three arguments:[19]

1. Pivotal cultural values attaching to the natural/cultivated environment rely on an area's unique character that cannot be addressed by methods that use universal scientific parameters to determine ecological structures and functions.
2. If a natural/cultivated environment has symbolic meanings and cultural values the object of these values are not ecosystems but shaped phenomena like mountains, lakes, forests, and, mainly, symbolic landscapes.[20]
3. Those cultural values do result not from properties produced by ecosystems but are the product of a specific way of seeing within the given cultural framework of symbolic experience.[21]

Common International Classification of Ecosystem Services (CICES)

The **Common International Classification of Ecosystem Services (CICES)** is a classification scheme developed to accounting systems (like National counts etc.), in order to avoid double-counting of Suporting Services with others Provisioning and Regulating Services.

https://cices.eu/

Examples

The following examples illustrate the relationships between humans and natural ecosystems through the services derived from them:

- In New York City, where the quality of drinking water had fallen below standards required by the U.S. Environmental Protection Agency (EPA), authorities opted to restore the polluted Catskill Watershed that had previously provided the city with the ecosystem service of water purification. Once the input of sewage and pesticides to the watershed area was reduced, natural abiotic processes such as soil absorption and filtration of chemicals, together with biotic recycling via root systems and soil microorganisms, water quality improved to levels that met government standards. The cost of this investment in natural capital was estimated between $1–1.5 billion, which contrasted dramatically with the estimated $6–8 billion cost of constructing a water filtration plant plus the $300 million annual running costs.[22]
- Pollination of crops by bees is required for 15–30% of U.S. food production; most large-scale farmers import non-native honey bees to provide this service. One study [23] reports that in California's agricultural region, it was found that wild bees alone could provide partial or complete pollination services or enhance the services provided by honey bees through behavioral interactions. However, intensified agricultural practices can quickly erode pollination services through the loss of species. The remaining species are unable to compensate this. The results of this study also indicate that the proportion of chaparral and oak-woodland habitat available for wild bees within 1–2 km of a farm can stabilize and enhance the provision of pollination services. The presence of such ecosystem elements functions almost like an insurance policy for farmers.
- In watersheds of the Yangtze River (China), spatial models for water flow through different forest habitats were created to determine potential contributions for hydroelectric power in the region. By quantifying the relative value of ecological parameters (vegetation-soil-slope complexes), researchers were able to estimate the annual economic benefit of maintaining forests in the watershed for power services to be 2.2 times that if it were harvested once for timber.[24]
- In the 1980s, mineral water company Vittel (now a brand of Nestlé Waters) faced a critical problem. Nitrates and pesticides were entering the company's springs in northeastern France. Local farmers had intensified agricultural practices and cleared native vegetation that previously had filtered water before it seeped into the aquifer used by Vittel. This contamination threatened the company's right to use the "natural mineral water" label under French law.[25] In response to this business risk, Vittel developed an incentive package for farmers to improve their agricultural practices and consequently reduce water pollution that had affected Vittel's product. For example, Vittel provided subsidies and free technical assistance to farmers in exchange for farmers' agreement to enhance

pasture management, reforest catchments, and reduce the use of agrochemicals. This is an example of a payment for ecosystem services program.[26]

- It was counted that to plant 15 000 ha new woodland in the UK, if we consider only the value of timber, it would cost £79 000 000 which is more than the benefit of £65 000 000. If, however, we include all other benefits the trees in lowland could provide (like soil stabilization, wind deflection, recreation, food production, air purification, carbon storage, wildlife habitat, fuel production, cooling, flood prevention), the costs will increase due to displacing the profitable farmland (would be around £231 000 000) but will be overweight by benefits of £546 000 000.[27]
- In Europe, various projects are implemented in order to define the values of concrete ecosystems and to implement this concept into decision making process. For example, "LIFE Viva grass" project aims to do this with grasslands in Baltics.[28]

Ecology

Understanding of ecosystem services requires a strong foundation in ecology, which describes the underlying principles and interactions of organisms and the environment. Since the scales at which these entities interact can vary from microbes to landscapes, milliseconds to millions of years, one of the greatest remaining challenges is the descriptive characterization of energy and material flow between them. For example, the area of a forest floor, the detritus upon it, the microorganisms in the soil and characteristics of the soil itself will all contribute to the abilities of that forest for providing ecosystem services like carbon sequestration, water purification, and erosion prevention to other areas within the watershed. Note that it is often possible for multiple services to be bundled together and when benefits of targeted objectives are secured, there may also be ancillary benefits —the same forest may provide habitat for other organisms as well as human recreation, which are also ecosystem services.

The complexity of Earth's ecosystems poses a challenge for scientists as they try to understand how relationships are interwoven among organisms, processes and their surroundings. As it relates to human ecology, a suggested research agenda [23] for the study of ecosystem services includes the following steps:

1. identification of *ecosystem service providers* (*ESP*s)—species or populations that provide specific ecosystem services—and characterization of their functional roles and relationships;
2. determination of community structure aspects that influence how ESPs function in their natural landscape, such as compensatory responses that stabilize function and non-random extinction sequences which can erode it;
3. assessment of key environmental (abiotic) factors influencing the provision of services;
4. measurement of the spatial and temporal scales ESPs and their services operate on.

Recently, a technique has been developed to improve and standardize the evaluation of ESP functionality by quantifying the relative importance of different species in terms of their efficiency and abundance.[29] Such parameters provide indications of how species respond to changes in the environment (i.e. predators, resource availability, climate) and are useful for identifying species that are disproportionately important at providing ecosystem services. However, a critical drawback is that the technique does not account for the effects of interactions, which are often both complex and fundamental in maintaining an ecosystem and can involve species that are not readily detected as a priority. Even so, estimating the functional structure of an ecosystem and combining it with information about individual species traits can help us understand the resilience of an ecosystem amidst environmental change.

Many ecologists also believe that the provision of ecosystem services can be stabilized with biodiversity. Increasing biodiversity also benefits the variety of ecosystem services available to society. Understanding the relationship between biodiversity and an ecosystem's stability is essential to the management of natural resources and their services.

Redundancy hypothesis

The concept of ecological redundancy is sometimes referred to as *functional compensation* and assumes that more than one species performs a given role within an ecosystem.[30] More specifically, it is characterized by a particular species increasing its efficiency at providing a service when conditions are stressed in order to maintain aggregate stability in the ecosystem.[31]

However, such increased dependence on a compensating species places additional stress on the ecosystem and often enhances its susceptibility to subsequent disturbance. The redundancy hypothesis can be summarized as "species redundancy enhances ecosystem resilience".[32]

Another idea uses the analogy of rivets in an airplane wing to compare the exponential effect the loss of each species will have on the function of an ecosystem; this is sometimes referred to as *rivet popping*.[33] If only one species disappears, the loss of the ecosystem's efficiency as a whole is relatively small; however, if several species are lost, the system essentially collapses—similar to an airplane that lost too many rivets. The hypothesis assumes that species are relatively specialized in their roles and that their ability to compensate for one another is less than in the redundancy hypothesis. As a result, the loss of any species is critical to the performance of the ecosystem. The key difference is the rate at which the loss of species affects total ecosystem functioning.

Portfolio effect

A third explanation, known as the *portfolio effect*, compares biodiversity to stock holdings, where diversification minimizes the volatility of the investment, or in this case, the risk of instability of ecosystem services.[34] This is related to the idea of *response diversity* where a suite of species will exhibit differential responses to a given environmental perturbation. When considered together, they create a stabilizing function that preserves the integrity of a service.[35]

Several experiments have tested these hypotheses in both the field and the lab. In ECOTRON, a laboratory in the UK where many of the biotic and abiotic factors of nature can be simulated, studies have focused on the effects of earthworms and symbiotic bacteria on plant roots.[33] These laboratory experiments seem to favor the rivet hypothesis. However, a study on grasslands at Cedar Creek Reserve in Minnesota supports the redundancy hypothesis, as have many other field studies.[36]

Economics



Sustainable urban drainage pond near housing in Scotland. The filtering and cleaning of surface and waste water by natural vegetation is a form of ecosystem service.

There are questions regarding the environmental and economic values of ecosystem services.[37] Some people may be unaware of the environment in general and humanity's interrelatedness with the natural environment, which may cause misconceptions. Although environmental awareness is rapidly improving in our contemporary world, ecosystem capital and its flow are still poorly understood, threats continue to impose, and we suffer from the so-called 'tragedy of the commons'.[38] Many efforts to inform decision-makers of current versus future costs and benefits now involve organizing and translating scientific knowledge to economics, which articulate the consequences of our choices in comparable units of impact on human well-being.[39] An especially challenging aspect of this process is that interpreting ecological information collected from one spatial-temporal scale does not necessarily mean it can be applied at another; understanding the dynamics of ecological processes relative to ecosystem services is essential in aiding economic decisions.[40] Weighting factors such as a service's irreplaceability or bundled services can also allocate economic value such that goal attainment becomes more efficient.

The economic valuation of ecosystem services also involves social communication and information, areas that remain particularly challenging and are the focus of many researchers.[41] In general, the idea is that although individuals make decisions for any variety of reasons, trends reveal the aggregative preferences of a society, from which the economic value of services can be inferred and assigned. The six major methods for valuing ecosystem services in monetary terms are:[42]

- Avoided cost: Services allow society to avoid costs that would have been incurred in the absence of those services (e.g. waste treatment by wetland habitats avoids health costs)

- Replacement cost: Services could be replaced with man-made systems (e.g. restoration of the Catskill Watershed cost less than the construction of a water purification plant)
- Factor income: Services provide for the enhancement of incomes (e.g. improved water quality increases the commercial take of a fishery and improves the income of fishers)
- Travel cost: Service demand may require travel, whose costs can reflect the implied value of the service (e.g. value of ecotourism experience is at least what a visitor is willing to pay to get there)
- Hedonic pricing: Service demand may be reflected in the prices people will pay for associated goods (e.g. coastal housing prices exceed that of inland homes)
- Contingent valuation: Service demand may be elicited by posing hypothetical scenarios that involve some valuation of alternatives (e.g. visitors willing to pay for increased access to national parks)

A peer-reviewed study published in 1997 estimated the value of the world's ecosystem services and natural capital to be between US$16–54 trillion per year, with an average of US$33 trillion per year.[43] However, Salles (2011) indicates 'The total value of biodiversity is infinite, so having debate about what is the total value of nature is actually pointless because we can't live without it'.

Management and policy

Although monetary pricing continues with respect to the valuation of ecosystem services, the challenges in policy implementation and management are significant and multitudinous. The administration of common pool resources is a subject of extensive academic pursuit.[44][45][46][47][48] From defining the problems to finding solutions that can be applied in practical and sustainable ways, there is much to overcome. Considering options must balance present and future human needs, and decision-makers must frequently work from valid but incomplete information. Existing legal policies are often considered insufficient since they typically pertain to human health-based standards that are mismatched with necessary means to protect ecosystem health and services. To improve the information available, one suggestion has involved the implementation of an *Ecosystem Services Framework* (ESF[49]), which integrates the biophysical and socio-economic dimensions of protecting the environment and is designed to guide institutions through multidisciplinary information and jargon, helping to direct strategic choices.

Novel and expedient methods are needed to deal with managing Earth's ecosystem services. Local to regional collective management efforts might be considered appropriate for services like crop pollination or resources like water.[23][44] Another approach that has become increasingly popular over the last decade is the marketing of ecosystem services protection. Payment and trading of services is an emerging worldwide small-scale solution where one can acquire credits for activities such as sponsoring the protection of carbon sequestration sources or the restoration of ecosystem service providers. In some cases, banks for handling such credits have been established and conservation companies have even gone public on stock exchanges, defining an evermore parallel link with economic endeavors and opportunities for tying into social perceptions.[39] However, crucial for implementation are clearly defined land rights, which is often lacking in many developing countries.[50] In particular, many forest-rich developing countries suffering deforestation experience conflict between different forest stakeholders.[50] In addition, concerns for such global transactions include inconsistent compensation for services or resources sacrificed elsewhere and misconceived warrants for irresponsible use. Another approach has been focused on protecting ecosystem service 'hotspots'. Recognition that the conservation of many ecosystem services aligns with more traditional conservation goals (i.e. biodiversity) has led to the suggested merging of objectives for maximizing their mutual success. This may be particularly strategic when employing networks that permit the flow of services across landscapes, and might also facilitate securing the financial means to protect services through a diversification of investors.[51][52]

For example, in recent years there has been interest in the valuation of ecosystem services provided by shellfish production and restoration.[53] A keystone species, low in the food chain, bivalve shellfish such as oysters support a complex community of species by performing a number of functions essential to the diverse array of species that surround them. There is also increasing recognition that some shellfish species may impact or control many ecological processes; so much so that they are included on the list of "ecosystem engineers"—organisms that physically, biologically or chemically modify the environment around them in

ways that influence the health of other organisms.[54] Many of the ecological functions and processes performed or affected by shellfish contribute to human well-being by providing a stream of valuable ecosystem services over time by filtering out particulate materials and potentially mitigating water quality issues by controlling excess nutrients in the water.

Ecosystem-based adaptation (EbA)

Ecosystem-based adaptation or EbA is an emerging strategy for community development and environmental management that seeks to use an ecosystem services framework to help communities adapt to the effects of climate change. The Convention on Biological Diversity currently defines Ecosystem-Based Adaptation as "the use of biodiversity and ecosystem services to help people adapt to the adverse effects of climate change", which includes the use of "sustainable management, conservation and restoration of ecosystems, as part of an overall adaptation strategy that takes into account the multiple social, economic and cultural co-benefits for local communities".[55]

In 2001, the Millennium Ecosystem Assessment announced that humanity's impact on the natural world was increasing to levels never before seen, and that the degradation of the planet's ecosystems would become a major barrier to achieving the Millennium Development Goals. In recognition of this fact, Ecosystem-Based Adaptation seeks to use the restoration of ecosystems as a stepping-stone to improving the quality of life in communities experiencing the impacts of climate change. Specifically, this involves the restoration of ecosystems that provide the community with essential services, such as the provisioning of food and water and protection from storm surges and flooding. EbA interventions typically combine elements of both climate change mitigation and adaptation to global warming to help address the community's current and future needs.[56]

Collaborative planning between scientists, policy makers, and community members is an essential element of Ecosystem-Based Adaptation. By drawing on the expertise of outside experts and local residents alike, EbA seeks to develop unique solutions to unique problems, rather than simply replicating past projects.[55]

Estuarine and coastal ecosystem services

Ecosystem services are defined as the gains acquired by humankind from surroundings ecosystems. Four different types of ecosystem services have been distinguished by the scientific body: regulating services, provisioning services, cultural services and supporting services. An ecosystem does not necessarily offer all four types of services simultaneously; but given the intricate nature of any ecosystem, it is usually assumed that humans benefit from a combination of these services. The services offered by diverse types of ecosystems (forests, seas, coral reefs, mangroves, etc.) differ in nature and in consequence. In fact, some services directly affect the livelihood of neighboring human populations (such as fresh water, food or aesthetic value, etc.) while other services affect general environmental conditions by which humans are indirectly impacted (such as climate change, erosion regulation or natural hazard regulation, etc.).[57]

Estuarine and coastal ecosystems are both marine ecosystems. An estuary is defined as the area in which a river meets the sea or the ocean. The waters surrounding this area are predominantly salty waters or brackish waters; and the incoming river water is dynamically motioned by the tide. An estuary strip may be covered by populations of reed (or similar plants) and/or sandbanks (or similar form or land).

A coastal ecosystem occurs in areas where the sea or ocean waters meet the land.

Regulating services

Regulating services are the "benefits obtained from the regulation of ecosystem processes".[58] In the case of coastal and estuarine ecosystems, these services include climate regulation, waste treatment and disease control and natural hazard regulation.

Climate regulation

Both the biotic and abiotic ensembles of marine ecosystems play a role in climate regulation. They act as sponges when it comes to gases in the atmosphere, retaining large levels of CO_2 and other greenhouse gases (methane and nitrous oxide). Marine plants also use CO_2 for photosynthesis purposes and help in reducing the atmospheric CO_2. The oceans and seas absorb the heat from the atmosphere and redistribute it through the means of water currents, and atmospheric processes, such as evaporation and the reflection of light allow for the cooling and warming of the overlying atmosphere. The ocean temperatures are thus imperative to the regulation of the atmospheric temperatures in any part of the world: "without the ocean, the Earth would be unbearably hot during the daylight hours and frigidly cold, if not frozen, at night".[59]

Waste treatment and disease regulation

Another service offered by marine ecosystem is the treatment of wastes, thus helping in the regulation of diseases. Wastes can be diluted and detoxified through transport across marine ecosystems; pollutants are removed from the environment and stored, buried or recycled in marine ecosystems: "Marine ecosystems break down organic waste through microbial communities that filter water, reduce/limit the effects of eutrophication, and break down toxic hydrocarbons into their basic components such as carbon dioxide, nitrogen, phosphorus, and water".[59] The fact that waste is diluted with large volumes of water and moves with water currents leads to the regulation of diseases and the reduction of toxics in seafood.

Buffer zones

Coastal and estuarine ecosystems act as buffer zones against natural hazards and environmental disturbances, such as floods, cyclones, tidal surges and storms. The role they play is to "[absorb] a portion of the impact and thus [lessen] its effect on the land".[59] Wetlands, for example, and the vegetation it supports – trees, root mats, etc. – retain large amounts of water (surface water, snowmelt, rain, groundwater) and then slowly releases them back, decreasing the likeliness of floods.[60] Mangrove forests protect coastal shorelines from tidal erosion or erosion by currents; a process that was studied after the 1999 cyclone that hit India. Villages that were surrounded with mangrove forests encountered less damages than other villages that weren't protected by mangroves.[61]

Provisioning Services

Provisioning services consist of all "the products obtained from ecosystems". Marine ecosystems provide people with: wild & cultured seafood, fresh water, fiber & fuel and biochemical & genetic resources.

Marine products

Humans consume a large number of products originating from the seas, whether as a nutritious product or for use in other sectors: "More than one billion people worldwide, or one-sixth of the global population, rely on fish as their main source of animal protein. In 2000, marine and coastal fisheries accounted for 12 per cent of world food production".[62] Fish and other edible marine products – primarily fish, shellfish, roe and seaweeds – constitute for populations living along the coast the main elements of the local cultural diets, norms and traditions. A very pertinent example would be sushi, the national food of Japan, which consists mostly of different types of fish and seaweed.

Fresh water

Water bodies that are not highly concentrated in salts are referred to as 'fresh water' bodies. Fresh water may run through lakes, rivers and streams, to name a few; but it is most prominently found in the frozen state or as soil moisture or buried deep underground. Fresh water is not only important for the survival of humans, but also for the survival of all the existing species of animals, plants.

Raw materials

Marine creatures provide us with the raw materials needed for the manufacturing of clothing, building materials (lime extracted from coral reefs), ornamental items and personal-use items (luffas, art and jewelry): "The skin of marine mammals for clothing, gas deposits for energy production, lime (extracted from coral reefs) for building construction, and the timber of mangroves and coastal forests for shelter are some of the more familiar uses of marine organisms. Raw marine materials are utilized for non-essential goods as well, such as shells and corals in ornamental items".[62] Humans have also referred to processes within marine environments for the production of renewable energy: using the power of waves – or tidal power – as a source of energy for the powering of a turbine, for example. Oceans and seas are used as sites for offshore oil and gas installations, offshore wind farms.

Biochemical and genetic resources

Biochemical resources are compounds extracted from marine organisms for use in medicines, pharmaceuticals, cosmetics and other biochemical products. Genetic resources are the genetic information found in marine organisms that would later on be used for animal and plant breeding and for technological advances in the biological field. These resources are either directly taken out from an organism – such as fish oil as a source of omega3 –, or used as a model for innovative man-made products: "such as the construction of fiber optics technology based on the properties of sponges. ... Compared to terrestrial products, marine-sourced products tend to be more highly bioactive, likely due to the fact that marine organisms have to retain their potency despite being diluted in the surrounding sea-water".[62]

Cultural services

Cultural services relate to the non-material world, as they benefit the benefit recreational, aesthetic, cognitive and spiritual activities, which are not easily quantifiable in monetary terms.

Inspirational

Marine environments have been used by many as an inspiration for their works of art, music, architecture, traditions... Water environments are spiritually important as a lot of people view them as a means for rejuvenation and change of perspective. Many also consider the water as being a part of their personality, especially if they have lived near it since they were kids: they associate it to fond memories and past experiences. Living near water bodies for a long time results in a certain set of water activities that become a ritual in the lives of people and of the culture in the region.

Recreation and tourism

Sea sports are very popular among coastal populations: surfing, snorkeling, whale watching, kayaking, recreational fishing...a lot of tourists also travel to resorts close to the sea or rivers or lakes to be able to experience these activities, and relax near the water.

Science and education

A lot can be learned from marine processes, environments and organisms – that could be implemented into our daily actions and into the scientific domain. Although much is still yet to still be known about the ocean world: "by the extraordinary intricacy and complexity of the marine environment and how it is influenced by large spatial scales, time lags, and cumulative effects".[59]



Beach accommodated into a recreational area.

Supporting services

Supporting services are the services that allow for the other ecosystem services to be present. They have indirect impacts on humans that last over a long period of time. Several services can be considered as being both supporting services and regulating/cultural/provisioning services.

Nutrient cycling

Nutrient cycling is the movement of nutrients through an ecosystem by biotic and abiotic processes.[63] The ocean is a vast storage pool for these nutrients, such as carbon, nitrogen and phosphorus. The nutrients are absorbed by the basic organisms of the marine food web and are thus transferred from one organism to the other and from one ecosystem to the other. Nutrients are recycled through the life cycle of organisms as they die and decompose, releasing the nutrients into the neighboring environment. "The service of nutrient cycling eventually impacts all other ecosystem services as all living things require a constant supply of nutrients to survive".[59]

Biologically mediated habitats

Biologically mediated habitats are defined as being the habitats that living marine structures offer to other organisms.[64] These need not to be designed for the sole purpose of serving as a habitat, but happen to become living quarters whilst growing naturally. For example, coral reefs and mangrove forests are home to numerous species of fish, seaweed and shellfish... The importance of these habitats is that they allow for interactions between different species, aiding the provisioning of marine goods and services. They are also very important for the growth at the early life stages of marine species (breeding and bursary spaces), as they serve as a food source and as a shelter from predators.

Primary production

Primary production refers to the production of organic matter, i.e., chemically bound energy, through processes such as photosynthesis and chemosynthesis. The organic matter produced by primary producers forms the basis of all food webs. Further, it generates oxygen (O2), a molecule necessary to sustain animals and humans.[65][66][67][68] On average, a human consumes about 550 liter of oxygen per day, whereas plants produce 1,5 liter of oxygen per 10 grams of growth.[69]



Coral and other living organisms serve as habitats for many marine species.

Businessworld

Ecosystem services degradation can pose a number of risks to corporate performance as well as provide business opportunities through ecosystem restoration and enhancement. Risks and opportunities include:

- ***Operational***
 - Risks such as higher costs for freshwater due to scarcity or lower output for hydroelectric facilities due to siltation
 - Opportunities such as increasing water-use efficiency or building an on-site wetland to circumvent the need for new water treatment infrastructure
- ***Regulatory and legal***
 - Risks such as new fines, government regulations, or lawsuits from local communities that lose ecosystem services due to corporate activities
 - Opportunities such as engaging governments to develop policies and incentives to protect or restore ecosystems that provide services a company needs
- ***Reputational***

- Risks such as retail companies being targeted by nongovernmental organization campaigns for purchasing wood or paper from sensitive forests

 Opportunities such as implementing and communicating sustainable purchasing, operating, or investment practices in order to differentiate corporate brands.

- ***Market and product***
 - Risks such as customers switching to other suppliers that offer products with lower ecosystem impacts or governments implementing new sustainable procurement policies
 - Opportunities such as launching new products and services that reduce customer impacts on ecosystems or participating in emerging markets for carbon sequestration and watershed protection other products
- ***Financing***
 - Risks such as banks implementing more rigorous lending requirements for corporate loans
 - Opportunities such as banks offering more favorable loan terms or investors taking positions in companies supplying products and services that improve resource use efficiency or restore degraded ecosystems

Many companies are not fully aware of the extent of their dependence and impact on ecosystems and the possible ramifications. Likewise, environmental management systems and environmental due diligence tools are more suited to handle "traditional" issues of pollution and natural resource consumption. Most focus on environmental impacts, not dependence. Several newly developed tools and methodologies can help the private sector value and assess ecosystem services. These include Our Ecosystem,[70] the Corporate Ecosystem Services Review (ESR),[71] Artificial Intelligence for Ecosystem Services (ARIES),[72] the Natural Value Initiative (NVI)[73] and InVEST (Integrated Valuation of Ecosystem Services & Tradeoffs) [74]

Land use change decisions

Ecosystem services decisions require making complex choices at the intersection of ecology, technology, society and the economy. The process of making ecosystem services decisions must consider the interaction of many types of information, honor all stakeholder viewpoints, including regulatory agencies, proposal proponents, decision makers, residents, NGOs, and measure the impacts on all four parts of the intersection. These decisions are usually spatial, always multi-objective, and based on uncertain data, models, and estimates. Often it is the combination of the best science combined with the stakeholder values, estimates and opinions that drive the process.[75]

One analytical study modeled the stakeholders as agents to support water resource management decisions in the Middle Rio Grande basin of New Mexico. This study focused on modeling the stakeholder inputs across a spatial decision, but ignored uncertainty.[76] Another study used Monte Carlo methods to exercise econometric models of landowner decisions in a study of the effects of land-use change. Here the stakeholder inputs were modeled as random effects to reflect the uncertainty.[77] A third study used a Bayesian decision support system to both model the uncertainty in the scientific information Bayes Nets and to assist collecting and fusing the input from stakeholders. This study was about siting wave energy devices off the Oregon Coast, but presents a general method for managing uncertain spatial science and stakeholder information in a decision making environment.[78] Remote sensing data and analyses can be used to assess the health and extent of land cover classes that provide ecosystem services, which aids in planning, management, monitoring of stakeholders' actions, and communication between stakeholders.[79]

In Baltic countries scientists, nature conservationists and local authorities are implementing integrated planning approach for grassland ecosystems (http://vivagrass.eu/about-the-project/). They are developing Integrated Planning Tool that will be based on GIS (geographic information system) technology and put online that will help for planners to choose the best grassland management solution for concrete grassland. It will look holistically at the processes in the countryside and help to find best grassland management solutions by taking into account both natural and socioeconomic factors of the particular site.

See also

- Blue carbon
- Biodiversity banking
- Controlled Ecological Life Support System
- Diversity-function debate
- Earth Economics
- Ecological goods and services
- Environmental finance
- Existence value
- Forest farming
- Environmental and economic benefits of having indigenous peoples tend land
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
- Mitigation banking
- Natural Capital
- Non-timber forest product
- Oxygen cycle
- Rangeland Management
- Soil functions
- Spaceship Earth
- Nature Based Solutions

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Insects as food

Insects as food or **edible insects** are insect species used for human consumption, e.g., whole or as an ingredient in processed food products such as burger patties, pasta, or snacks. The cultural and biological process of eating insects (by humans as well as animals) is described as entomophagy.



Whole, fried edible insects as street food in Germany

Contents

Edible insects
- Frequently consumed insect species
- Edible insects for industrialized mass production

Nutritional profile

Farming, production, and processing
- Insect food products

Food safety
- Challenges and safety concerns
- Regulation and authorisation
 - Switzerland
 - EU

Awareness

See also

Footnotes

External links

Further reading

Edible insects

Frequently consumed insect species

Estimates of numbers of edible insect species consumed globally range from 1,000 to 2,000.[1] These species include 235 butterflies and moths, 344 beetles, 313 ants, bees and wasps, 239 grasshoppers, crickets and cockroaches, 39 termites, and 20 dragonflies, as well as cicadas.[2] Which species are consumed varies by region due to differences in environment, ecosystems, and climate.

The table below lists the top five insect orders consumed by humans worldwide, retrieved from *Edible Insects: Future Prospects for Food and Feed Security* by Arnold van Huis, Joost Van Itterbeeck, Harmke Klunder, Esther Mertens, Afton Halloran, Giulia Muir and Paul Vantomme.[3]

Order of insect	Common name	Consumption rate worldwide by human population (%)
Coleoptera	Beetles	31
Lepidoptera	Butterflies, moths	18
Hymenoptera	Bees, wasps, ants	14
Orthoptera	Grasshoppers, locusts, crickets	13
Hemiptera	Cicadas, leafhoppers, planthoppers	10

For a list of edible insects consumed locally see: List of edible insects by country.

Edible insects for industrialized mass production

In Western markets such as Europe and North America, academics as well as large-scale insect food producers such as *Entomofarms* in Canada, *Aspire Food Group* in the United States,[4] *Protifarm* in the Netherlands, and *Bühler Group* in Switzerland, focus on four insects species suitable for human consumption as well as industrialized mass production:[5]

- House cricket (*Acheta domesticus*)
- European migratory locust (*Locusta migratoria*)
- Mealworms (*Tenebrio molitor*) as larvae
- Lesser mealworms (*Alphitobius diaperinus*) as larvae, mostly marketed under the term buffalo worms.



Freeze-dried house crickets as food (or food ingredient)



Mealworms as food (or food ingredient)



Buffalo worms as food (or ingredient)

Nutritional profile

Insects are nutrient efficient compared to other meat sources. Insects such as crickets are a complete protein and contain a useful amount, comparable with protein from soybeans, though less than in casein (found in foods such as cheese).[6] They have dietary fiber and include mostly unsaturated fat and contain some vitamins, such as vitamin B12[7], riboflavin and vitamin A, and essential minerals.[8][9]



Freeze-dried mealworms and buffalo worms (lesser mealworm)

Locusts contain between 8 and 20 milligrams of iron for every 100 grams of raw locust. Beef on the other hand contains roughly 6 milligrams of iron in the same amount of meat. Crickets as well are very efficient in terms of nutrients. For every 100 grams of substance crickets contain 12.9 grams of protein, 121 calories, and 5.5 grams of fat. Beef contains more protein containing 23.5 grams

in 100 grams of substance, but also has roughly 3 times the calories, and four times the amount of fat as crickets do in 100 grams. So, per 100 grams of substance, crickets contain only half the nutrients of beef, except for iron. High levels of iron are implicated in bowel cancer[10] and heart disease.[11]

Nutritional value per 100 g	Mealworms (*Tenebrio molitor*)	Buffalo worms (*Alphitobius diaperinus*)	House crickets (*Acheta domesticus*)	Migratory locust (*Locusta migratoria*)
Energy	550 kcal / 2303 KJ	484 kcal/ 2027 KJ	458 kcal/ 1918 KJ	559 kcal/ 2341 KJ
Fat Of which saturated fatty acids	37,2 g 9 g	24,7 g 8 g	18,5 g 7 g	38,1 g 13,1 g
Carbohydrates Of which sugars	5,4 g 0 g	6,7 g 0 g	0 g 0 g	1,1 g 0 g
Protein	45,1 g	56,2 g	69,1 g	48,2 g
Salt	0,37 g	0,38 g	1,03 g	0,43 g

Farming, production, and processing

Edible insects are raised as livestock in specialized insect farms. In North American as well as European countries such as the Netherlands or Belgium, insects are produced under strict food law and hygiene standard for human consumption.



Crickets being raised for human consumption

Several variables apply, such as temperature, humidity, feed, water sources, housing, depending on the insect species. The insects are raised from eggs to larvae status (mealworms, lesser mealworms) or to their mature form (crickets, locusts), and then killed, in industrialized insect farms by lowering the temperature.[12][13] After that the insects are freeze-dried and packed whole, or pulverized to insect powder (insect flour), to be processed in other food products such as bakery products, or snacks.

Aside from nutritional composition and digestibility, insects are also selected for ease of rearing by the producer. This includes susceptibility to disease, efficiency of feed conversion, developmental rate and generational turnover.[14]

Insect food products

The following processed food products are produced by several producers in North America, Canada, and the EU:

- *Insect flour*: Pulverized, freeze-dried insects (e.g., cricket flour).
- *Insect burger*: Hamburger patties made from insect powder / insect flour (mainly from worms or from house cricket) and further ingredients.[15]
- *Insect fitness bars*: Protein bars containing insect powder (mostly house crickets).
- *Insect pasta*: Pasta made of wheat flour, fortified with insect flour (house crickets or mealworms).
- *Insect bread* (Finnish *Sirkkaleipä*): Bread baked with insect flour (mostly house crickets).[16]



Insect burger made by Essento containing mealworms



Fusilli made of cricket flour



Snack made of cricket flour

Food safety

Challenges and safety concerns

In spite of all the advantages that insect protein are provided, there are some potential challenges caused by production and safety concerns.

Mass production in the insect industry is a concern due to a lack of technology and funds to efficiently harvest, and produce insects. The machinery would have to house proper enclosure for each life cycle of the insect as well as the temperature control as that is key for insect development.[17]

The industry also has to consider the shelf life of insects in comparison to animal products as that some can have food safety concerns. Insects have the capability of accumulating potential hazards, such as contaminants, pathogens, the concentration of heavy metals, allergens, and pesticides etc.[18]

Table below combined the data from two studies[19][20] published in Comprehensive Reviews in Food Science and Food Safety, and summarized the potential hazards of the top five insect species consumed by humans.

Insect order	Common name	Hazard category	Potential hazard
Coleoptera	Beetle	Chemical	Oromones
			Cyanogentic substances
			Heavy metal contamination
Lepidoptera	Silkworm	Allergic	
		Chemical	Thiaminase
	Honeycomb moth	Microbial	High bacterial count
		Chemical	Cyanogentic substances
Hymenoptera	Ant	Chemical	Antinutritional factors (tannin, phytate)
Orthoptera	House cricket	Microbial	High bacterial count
Hemiptera		Parasitical	Chagas disease
Diptera	Black soldier fly	Parasitical	Myiasis

Hazards in insects that are shown above can be controlled by various ways. Allergic hazard can be labelled on the package to avoid consumption by allergy susceptible consumers. Selective farming can be used to minimize chemical hazard, whereas microbial and parasitical hazard can be controlled by cooking processes.[21]

Regulation and authorisation

Switzerland

On 1 May 2017, Switzerland has approved the following insect species as food:[22]

- House cricket (*Acheta domesticus*)
- European locust (*Locusta migratoria*)
- Mealworms (*Tenebrio molitor*) as larvae

Under certain conditions, these may be offered to consumers as whole animals, pulverized, or processed in food products.

EU

In the EU, insects fall within the definition of novel food as food ingredients isolated from animals, given by the European Commission. Parts of insects, e.g., legs, wings, or heads, as well as whole insects, fall within this definition.[23] Dossiers for several insects species are currently under review by the European Food Safety Authority. In August 2018, EFSA published a risk profile for the house cricket as food.[24]

Awareness

The World Edible Insect Day, being held on 23 October, was introduced by Belgian entrepreneur Chris Derudder in 2015 to raise awareness globally for the consumption of edible insects, with a focus on Europe, North America, and Australia.[25]

See also

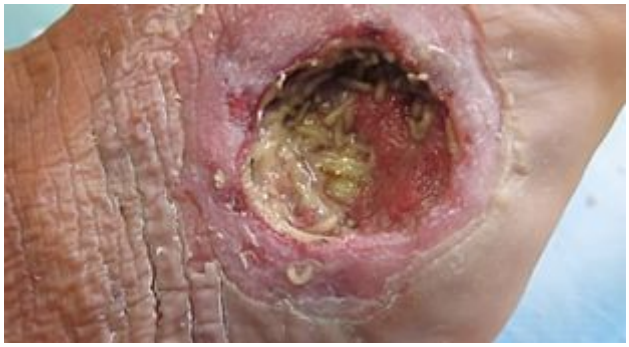
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Insects in medicine

Insects have long been used in medicine, both traditional and modern, sometimes with little evidence of their effectiveness. For the purpose of the article, and in line with custom, medicinal uses of other arthropods such as spiders are included.



Maggot debridement therapy on a wound on a diabetic foot

Contents

Traditional and alternative uses
- Traditional Chinese medicine
- India and Ayurveda
- Africa
- Americas
- Honey bee products

Modern scientific uses
- Maggot therapy
- Apitherapy
- Blister beetle and Spanish fly
- Blood-feeding insects

Arachnids
- Psychoactive scorpions

References

Traditional and alternative uses

The medicinal uses of insects and other arthropods worldwide have been reviewed by Meyer-Rochow [1], who provides examples of all major insect groups,spiders, worms and molluscs and discusses their potential as suppliers of bioactive components. Using insects (and spiders) to treat various maladies and injuries has a long tradition and, having stood the test of time, can be effective and provide results. However, sometimes folk-medicinal "logic" was based on the Doctrine of Signatures = "let likes be cured by likes"and had, if any at all, little more than a psychological effect. For example, to treat cases of constipation, dung beetles were prescribed; to slim down stick insects were thought to help; hairy tarantulas seemed the right treatment for hair loss and fat grubs resembling the swollen limb caused by the parasite Wucheria bancrofti were expected to help the elephantiasis sufferer. An organism bearing parts that resemble human body parts, animals, or other objects, was thought to have useful relevance to those parts, animals or objects. So, for example, the femurs of grasshoppers, which were said to resemble the human liver, were used to treat liver ailments by the indigenous peoples of Mexico.[2] This doctrine is common throughout traditional and alternative medicine, but is most prominent where medical traditions are broadly accepted, as in traditional Chinese medicine and Ayurveda, and less by community and family based medicine, as is more common in parts of Africa.

Traditional Chinese medicine

Traditional Chinese medicine includes the use of herbal medicine, acupuncture, massage, exercise, and dietary therapy. It is a typical component of modern medical care throughout East Asia and in some parts of Southeast Asia (such as Thailand). Insects are very commonly incorporated as part of the herbal medicine component of traditional Chinese medicine, and their medical

properties and applications are broadly accepted and agreed upon. Some brief examples follow:

The Chinese Black Mountain Ant, *Polyrhachis vicina*, is supposed to act as a cure all and is widely used, especially by the elderly. It is said to prolong life, to have anti-aging properties, to replenish Qi, and to increase virility and fertility. Recent interest in the ants' medicinal qualities has led to British researchers to study the extract's potential to serve as a cancer-fighting agent.[3] Chinese Black Mountain Ant extract is typically consumed mixed with wine.

India and Ayurveda

Ayurveda is ancient traditional Indian treatment almost universally incorporated alongside Western medicine as a typical component of medical treatment in India. Although Ayurvedic medicine is often effective, doses can be inconsistent, and may sometimes be contaminated with toxic heavy metals.[4] Some brief examples to follow:

Termite is said to cure a variety of diseases, both specific and vague. Typically the mound or a portion of the mound is dug up and the termites and the architectural components of the mound are together ground into a paste which is then applied topically to the affected areas or, more rarely, mixed with water and consumed.[5] This treatment was said to cure ulcers, rheumatic diseases, and anemia.[4] It was also suggested to be a general pain reliever and health improver.[4]

The Jatropha Leaf Miner, a lepidopteran which feeds preferentially on *Jatropha*, is an example of a major insect agricultural pest which is also a medicinal remedy.[5] The larvae, which are also the form of the insect with the greatest economic impact on agriculture, are harvested, boiled, and mashed into a paste which is administered topically and is said to induce lactation, reduce fever, and soothe gastrointestinal tracts.[5]

Africa

Unlike China and India, the traditional insect medicine of Africa is extremely variable. It is largely regional, with few, if any, major agreements on which insects are useful as treatments for which ailments.[5] Most insect medicinal treatments are passed on through communities and families, rather than being taught in university settings, as Traditional Chinese Medicine and Ayurveda sometimes are; furthermore, most traditional medicine practices necessitate a person in a "healer" role.[5] Some brief examples to follow:

Grasshopper is both commonly eaten as a delicacy and an excellent source of protein *and* is consumed for medicinal purposes.[5] These insects are typically collected, dried in the sun, and then ground into a powder.[5] The powder can then be turned into a paste when mixed with water and ash and applied to the forehead to alleviate the pain of violent headaches.[5] Additionally, the headaches themselves can be prevented by a "healer" inserting the paste under the skin at the nape of the afflicted person's neck.[5]

Termites are also used in parts of Africa much like they are in India.[4] Parts of the mound are dug up, boiled, and turned into a paste, which can then be applied to external wounds to prevent infection or consumed to treat internal hemorrhages.[5] termites are used not only as a form of medicine, but also as a medical device. If a "healer" wants to insert a medicine subcutaneously, they will often spread that medicine on the skin of the patient, and then agitate a termite and place the insect on the skin of the patient.[5] When the termite bites, its mandibles effectively serve as an injection device.[5]

Americas

The Americas were more highly influenced by the Doctrine of Signatures than China, India, or Africa, most likely because of their colonial history with Europe. The majority of insect use in medicine is associated with Central America and parts of South America, rather than North America, and most of it is based on the medical techniques of indigenous peoples.[2] Currently, insect

medicine is practiced much more rarely than in China, India, or Africa, though it is still relatively common in rural areas with large indigenous populations.[2] Some examples to follow:

Chapulines, or grasshoppers, are commonly consumed as a toasted regional dish in some parts of Mexico, but they are also used medicinally.[2] They are said to serve as diuretic to treat kidney diseases, to reduce swelling, and to relieve the pain of intestinal disorders when they are consumed.[2] However, there are some risks associated with consuming chapulines, as they are known to harbor nematodes which may be transmitted to humans upon consumption.

Much like the termites of Africa, ants were sometimes used as medicinal devices by the indigenous peoples of Central America.[2] The soldier cast of the Army ant would be collected and used as living sutures by Mayans.[2] This involved agitating an ant and holding its mandibles up to the wound edges; when it bit down, the thorax and abdomen were removed, leaving the head holding the wound together.[2] The ant's salivary gland secretions were reputed to have antibiotic properties.[2] The venom of the Red harvester ant was used to treat rheumatism, arthritis, and poliomyelitis via the immunological reaction produced by its sting. This technique, in which ants are allowed to sting afflicted areas in a controlled manner, is still used in some arid rural areas of Mexico.[2]

The silkworm, *Bombyx mori*, was also commonly consumed both as a regional food and for medicinal purposes in Central America after it was brought to the New World by the Spanish and Portuguese.[2] Only the immatures are consumed. Boiled pupae were eaten to treat apoplexy, aphasy, bronchitis, pneumonia, convulsions, hemorrhages, and frequent urination.[2] The excrement produced by the larvae is also eaten to improve circulation and alleviate the symptoms of cholera (intense vomiting and diarrhea).[2]

Honey bee products

Honey bee products are used medicinally across Asia, Europe, Africa, Australia, and the Americas, despite the fact that the honey bee was not introduced to the Americas until the colonization by Spain and Portugal. They are by far the most common medical insect product, both historically and currently.[5]

Honey is the most frequently referenced medical bee material. It can be applied to skin to treat excessive scar tissue, rashes, and burns,[6] and can be applied as a poultice to eyes to treat infection.[4] It is also consumed for digestive problems and as a general health restorative, and can be heated and consumed to treat head colds, cough, throat infections, laryngitis, tuberculosis, and lung diseases.[2]

Additionally, apitoxin, or honey bee venom, can be applied via direct stings to relieve arthritis, rheumatism, polyneuritis, and asthma.[2] Propolis, a resinous, waxy mixture collected by honeybees and used as a hive insulator and sealant, is often consumed by menopausal women because of its high hormone content, and it is said to have antibiotic, anesthetic, and anti-inflammatory properties.[2] Royal jelly is used to treat anemia, gastrointestinal ulcers, arteriosclerosis, hypo- and hypertension, and inhibition of sexual libido.[2] Finally Bee bread, or bee pollen, is eaten as a generally health restorative, and is said to help treat both internal and external infections.[2] All of these honey bee products are regularly produced and sold, especially online and in health food stores, though none are yet approved by the FDA.

Modern scientific uses

Though insects were widely used throughout history for medical treatment on nearly every continent, relatively little medical entomological research has been conducted since the revolutionary advent of antibiotics. Heavy reliance on antibiotics, coupled with discomfort with insects in Western culture limited the field of insect pharmacology until the rise of antibiotic resistant infections sparked pharmaceutical research to explore new resources. Arthropods represent a rich and largely unexplored source of new medicinal compounds.[7]

Maggot therapy

Maggot therapy is the intentional introduction of live, disinfected blow fly larvae (maggots) into soft tissue wounds to selectively clean out the necrotic tissue. This helps to prevent infection; it also speeds healing of chronically infected wounds and ulcers.[8] Military surgeons since classical antiquity noticed that wounds which had been left untreated for several days, and which had become infested with maggots, healed better than wounds not so infested.[9] Maggots secrete several chemicals that kill microbes, including allantoin, urea, phenylacetic acid, phenylacetaldehyde, calcium carbonate, proteolytic enzymes, and many others.[10]

Maggots were used for wound healing by the Maya and by indigenous Australians. More recently, they were used in Renaissance Europe, in the Napoleonic Wars, the American Civil War, and in the First and Second World Wars.[11][12] It continues to be used in military medicine.[13]

Apitherapy

Apitherapy is the medical use of honeybee products such as honey, pollen, bee bread, propolis, royal jelly and bee venom. One of the major peptides in bee venom, called Melittin, has the potential to treat inflammation in sufferers of Rheumatoid arthritis and Multiple sclerosis. Melittin blocks the expression of inflammatory genes, thus reducing swelling and pain. It is administered by direct insect sting, or intramuscular injections. Bee products demonstrate a wide array of antimicrobial factors and in laboratory studies and have been shown to kill antibiotic resistant bacteria, pancreatic cancer cells, and many other infectious microbes.[14]

Blister beetle and Spanish fly

Spanish fly is an emerald-green beetle, *Lytta vesicatoria*, in the blister beetle family (Meloidae). It and other such species were used in preparations offered by traditional apothecaries. The insect is the source of the terpenoid cantharidin, a toxic blistering agent once used as an aphrodisiac.[15][16]

Blood-feeding insects

Many blood-feeding insects like ticks, horseflies, and mosquitoes inject multiple bioactive compounds into their prey. These insects have been used by practitioners of Eastern Medicine for hundreds of years to prevent blood clot formation or thrombosis.[17] However, modern medical research has only recently begun to investigate the drug development potential of blood-feeding insect saliva. These compounds in the saliva of blood feeding insects are capable of increasing the ease of blood feeding by preventing coagulation of platelets around the wound and provide protection against the host's immune response. Currently, over 1280 different protein families have been associated with the saliva of blood feeding organisms.[18] This diverse range of compounds may include:[14][19]

- inhibitors of platelet aggregation, ADP, arachidonic acid, thrombin, and PAF.
- anticoagulants
- vasodilators
- vasoconstrictors
- antihistamines
- sodium channel blockers
- complement inhibitors
- pore formers
- inhibitors of angiogenesis
- anaesthetics
- AMPs and microbial pattern recognition molecules.
- Parasite enhancers/activators

Currently, some preliminary progress has been made with investigation of the therapeutic properties of tick anticoagulant peptide (TAP) and Ixolaris a novel recombinant tissue factor pathway inhibitor (TFPI) from the salivary gland of the tick, *Ixodes scapularis*.[20] Additionally, Ixolaris, a tissue factor inhibitor has been shown to block primary tumor growth and angiogenesis in a glioblastoma model.[21] Despite the strong potential of these compounds for use as anticoagulants or immunomodulating drugs no modern medicines, developed from the saliva of blood-sucking insects, are currently on the market.[14]

Arachnids

Like plants and insects, arachnids have also been used for thousands of years in traditional medical practices. Recent scientific research in natural bioactive factors has increased, leading to a renewed interest in venom components in many animals. In 1993 Margatoxin was synthesized from the venom of the *Centruroides margaritatus* the Central American bark scorpion. It is a peptide that selectively inhibits voltage-dependent potassium channels. Patented by Merck, it has the potential to prevent neointimal hyperplasia, a common cause of bypass graft failure.[22]

In addition to medical uses of arachnid defense compounds, a great amount of research has recently been directed toward the synthesis and use of spider silk as a scaffolding for ligament generation. Spider silk is an ideal material for the synthesis of medical skin grafts or ligament implants because it is one of the strongest known natural fibers and triggers little immune response in animals. Spider silk may also be used to make fine sutures for stitching nerves or eyes to heal with little scarring. Medical uses of spider silk is not a new idea. Spider silks have been used for thousands of years to fight infection and heal wounds. Efforts to produce industrial quantities and qualities of spider silk in transgenic goat milk are underway.[23][24]

Psychoactive scorpions

Recent news reports[25] claim that use of scorpions for psychoactive purposes is gaining in popularity in Asia. Heroin addicts in Afghanistan are purported to smoke dried scorpions or use scorpion stings to get high when heroin is not available. The 'scorpion sting craze' has also increased in India with a decreasing availability of other drugs and alcohol available to youth.[26] Young people are reportedly flocking to highway sides where they can purchase scorpion stings that after several minutes of intense pain, supposedly produce a six- to eight-hour feeling of wellbeing.[27]

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Human interactions with insects

Human interactions with insects include both a wide variety of uses, whether practical such as for food, textiles, and dyestuffs, or symbolic, as in art, music, and literature, and negative interactions including serious damage to crops and extensive efforts to eliminate insect pests.



The "Spanish fly", *Lytta vesicatoria*, has been considered to have medicinal, aphrodisiac, and other properties.

Academically, the interaction of insects and society has been treated in part as **cultural entomology**, dealing mostly with "advanced" societies, and in part as **ethnoentomology**, dealing mostly with "primitive" societies, though the distinction is weak and not based on theory. Both academic disciplines explore the parallels, connections and influence of insects on human populations, and vice versa. They are rooted in anthropology and natural history, as well as entomology, the study of insects. Other cultural uses of insects, such as biomimicry, do not necessarily lie within these academic disciplines.

More generally, people make a wide range of uses of insects, both practical and symbolic. On the other hand, attitudes to insects are often negative, and extensive efforts are made to kill them. The widespread use of insecticides has failed to exterminate any insect pest, but has caused resistance to commonly-used chemicals in a thousand insect species.

Practical uses include as food, in medicine, for the valuable textile silk, for dyestuffs such as carmine, in science, where the fruit fly is an important model organism in genetics, and in warfare, where insects were successfully used in the Second World War to spread disease in enemy populations. One insect, the honey bee, provides honey, pollen, royal jelly, propolis and an anti-inflammatory peptide, melittin; its larvae too are eaten in some societies. Medical uses of insects include maggot therapy for wound debridement. Over a thousand protein families have been identified in the saliva of blood-feeding insects; these may provide useful drugs such as anticoagulants, vasodilators, antihistamines and anaesthetics.

Symbolic uses include roles in art, in music (with many songs featuring insects), in film, in literature, in religion, and in mythology. Insect costumes are used in theatrical productions and worn for parties and carnivals.

Contents

Context
- Culture
- Cultural entomology and ethnoentomology

Benefits and costs
- Insect ecosystem services
- Pests and propaganda

Practical uses
- As food
- In medicine
- In science and technology

In textiles
In warfare

Symbolic uses
In mythology and folklore
In religion
In art
In literature and film
In music
In astronomy and cosmology
In costumes

See also

References

Further reading

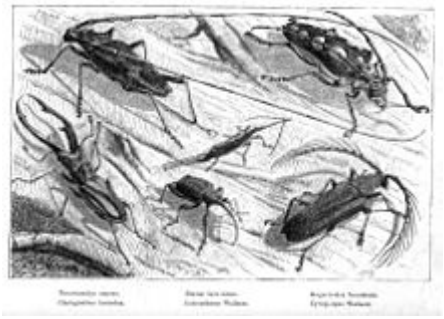
External links

Context

Culture

Culture consists of the social behaviour and norms found in human societies and transmitted through social learning. Cultural universals in all human societies include expressive forms like art, music, dance, ritual, religion, and technologies like tool usage, cooking, shelter, and clothing. The concept of material culture covers physical expressions such as technology, architecture and art, whereas immaterial culture includes principles of social organization, mythology, philosophy, literature, and science.[1] This article describes the roles played by insects in human culture so defined.

Cultural entomology and ethnoentomology



"Remarkable Beetles Found at Simunjon, Borneo": Alfred Russel Wallace was a pioneer of ethnoentomology.

Ethnoentomology developed from the 19th century with early works by authors such as Alfred Russel Wallace (1852) and Henry Walter Bates (1862). Hans Zinsser's classic *Rats, Lice and History* (1935) showed that insects were an important force in human history. Writers like William Morton Wheeler, Maurice Maeterlinck, and Jean Henri Fabre described insect life and communicated their meaning to people "with imagination and brilliance". Frederick Simon Bodenheimer's *Insects as Human Food* (1951) drew attention to the scope and potential of entomophagy, and showed a positive aspect of insects. Food is the most studied topic in ethnoentomology, followed by medicine and beekeeping.[2]

In 1968, Erwin Schimitschek claimed cultural entomology as a branch of insect studies, in a review of the roles insects played in folklore and culture including religion, food, medicine and the arts.[3] In 1984, Charles Hogue covered the field in English and from 1994 to 1997, Hogue's *The Cultural Entomology Digest* served as a forum on the field.[4][5] Hogue argued that "Humans spend their intellectual energies in three basic areas of activity: surviving, using practical learning (the application of technology); seeking pure knowledge through inductive mental processes (science); and pursuing enlightenment to taste a pleasure by aesthetic exercises that may be referred to as the 'humanities.' Entomology has long been concerned with survival (economic entomology) and scientific study (academic entomology), but the branch of investigation that addresses the influence of insects (and other terrestrial Arthropoda, including arachnids and myriapods) in literature, language, music, the arts,

interpretive history, religion, and recreation has only become recognized as a distinct field" through Schimitschek's work.[3][6][7] Hogue set out the boundaries of the field by saying: "The narrative history of the science of entomology is not part of cultural entomology, while the influence of insects on general history would be considered cultural entomology."[8] He added: "Because the term "cultural" is narrowly defined, some aspects normally included in studies of human societies are excluded."[8]



Fighting insects: an agricultural aircraft applies low-insecticide bait to kill western corn rootworms.

Darrell Addison Posey, noting that the boundary between cultural entomology and ethnoentomology is difficult to draw, cites Hogue as limiting cultural entomology to the influence of insects on "the essence of humanity as expressed in the arts and humanities". Posey notes further that cultural anthropology is usually restricted to the study of "advanced", industrialised, and literate societies, whereas ethnoentomology studies "the entomological concerns of 'primitive' or 'noncivilized' societies". Posey states at once that the division is artificial, complete with an unjustified us/them bias.[2] Brian Morris similarly criticises the way that anthropologists treat non-Western attitudes to nature as monadic and spiritualist, and contrast this "in gnostic fashion" with a simplistic treatment of Western, often 17th-century, mechanistic attitude. Morris considers this "quite unhelpful, if not misleading", and offers instead his own research into the multiple ways that the people of Malawi relate to insects and other animals: "pragmatic, intellectual, realist, practical, aesthetic, symbolic and sacramental."[9]

Benefits and costs

Insect ecosystem services



Pollination, here by a bee on an avocado crop, is an ecosystem service.

The Millennium Ecosystem Assessment (MEA) report 2005 defines ecosystem services as benefits people obtain from ecosystems, and distinguishes four categories, namely provisioning, regulating, supporting, and cultural. A fundamental tenet is that a few species of arthropod are well understood for their influence on humans (such as honeybees, ants, mosquitoes, and spiders). However, insects offer ecological goods and services.[10] The Xerces Society calculates the economic impact of four ecological services rendered by insects: pollination, recreation (i.e. "the importance of bugs to hunting, fishing, and wildlife observation, including bird-watching"), dung burial, and pest control. The value has been estimated at $153 billion worldwide.[11] As the ant expert[12] E. O. Wilson observed: "If all mankind were to disappear, the world would regenerate back to the rich state of equilibrium that existed ten thousand years ago. If insects were to vanish, the environment would collapse into chaos."[13] A *Nova* segment on the American Public Broadcasting Service framed the relationship with insects in an urban context: "We humans like to think that we run the world. But even in the heart of our great cities, a rival superpower thrives ... These tiny creatures live all around us in vast numbers, though we hardly even notice them. But in many ways, it is they who really run the show.[14] *The Washington Post* stated: "We are flying blind in many aspects of preserving the environment, and that's why we are so surprised when a species like the honeybee starts to crash, or an insect we don't want, the Asian tiger mosquito or the fire ant, appears in our midst. In other words: Start thinking about the bugs."[15]

Pests and propaganda

Human attitudes toward insects are often negative, reinforced by sensationalism in the media.[16] This has produced a society that attempts to eliminate insects from daily life.[17] For example, nearly 75 million pounds of broad-spectrum insecticides are manufactured and sold each year for use in American homes and gardens. Annual revenues from insecticide sales to homeowners exceeded $450 million in 2004. Out of the roughly a million species of insects described so far, not more than 1,000 can be regarded as serious pests, and less than 10,000 (about 1%) are even occasional pests.[17] Yet not one species of insect has been permanently eradicated through the use of pesticides. Instead, at least 1,000 species have developed field resistance to pesticides, and extensive harm has been done to beneficial insects including pollinators such as bees.[18]



In the war against the potato beetle, East German Young Pioneers were urged to collect and kill Colorado beetles.

During the Cold War, the Warsaw Pact countries launched a widespread war against the potato beetle, blaming the introduction of the species from America on the CIA, demonising the species in propaganda posters, and urging children to gather the beetles and kill them.[19]

Practical uses

As food



Witchetty grubs were prized as food by Australian aborigines.

Entomophagy is the eating of insects. Many edible insects are considered a culinary delicacy in some societies around the world, and Frederick Simon Bodenheimer's *Insects as Human Food* (1951) drew attention to the scope and potential of entomophagy, but the practice is uncommon and even taboo in other societies. Sometimes insects are considered suitable only for the poor in the third world, but in 1975 Victor Meyer-Rochow suggested that insects could help ease global future food shortages and advocated a change in western attitudes towards cultures in which insects were appreciated as a food item.[20] P. J. Gullan and P. S. Cranston felt that the remedy for this may be marketing of insect dishes as suitably exotic and costly to make them acceptable. They also note that some societies in sub-Saharan Africa prefer caterpillars to beef, while Chakravorty et al. (2011)[21] point out that food insects (highly appreciated in North-East India) are more expensive than meat. The economics, i.e., the costs involved collecting food insects and the money earned through the sale of such insects, have been studied in a Laotian setting by Meyer-Rochow et al. (2008).[22] In Mexico, ant larvae and corixid water boatman eggs are sought out as a form of caviar by gastronomes. In Guangdong, water beetles fetch a high enough price for these insects to be farmed. Especially high prices are fetched in Thailand for the giant water bug *Lethocerus indicus*.[23]

Insects used in food include honey bee larvae and pupae,[24][25] mopani worms,[26] silkworms,[27] Maguey worms,[28] Witchetty grubs,[29] crickets,[30] grasshoppers[31] and locusts.[32] In Thailand, there are 20,000 farmers rearing crickets, producing some 7,500 tons per year.[33]

In medicine

Insects have been used medicinally in cultures around the world, often according to the Doctrine of Signatures. Thus, the femurs of grasshoppers, which were said to resemble the human liver, were used to treat liver ailments by the indigenous peoples of Mexico.[34] The doctrine was applied in both Traditional Chinese Medicine (TCM) and in Ayurveda. TCM uses arthropods for various purposes; for example, centipede is used to treat tetanus, seizures, and convulsions,[35] while the Chinese Black Mountain Ant, *Polyrhachis vicina*, is used as a cure all, especially by the elderly, and extracts have been examined as a possible anti-cancer

agent.[36] Ayurveda uses insects such as Termite for conditions such as ulcers, rheumatic diseases, anaemia, and pain. The Jatropha leaf miner's larvae are used boiled to induce lactation, reduce fever, and soothe the gastrointestinal tract.[21][37] In contrast, the traditional insect medicine of Africa is local and unformalised.[37] The indigenous peoples of Central America used a wide variety of insects medicinally. Mayans used Army ant soldiers as living sutures.[34] The venom of the Red harvester ant was used to cure rheumatism, arthritis, and poliomyelitis via the immune reaction produced by its sting.[34] Boiled *silkworm* pupae were taken to treat apoplexy, aphasy, bronchitis, pneumonia, convulsions, haemorrhages, and frequent urination.[34]



Army ants were used by the Mayans as living sutures, their powerful jaws holding a wound closed.

Honey bee products are used medicinally in apitherapy across Asia, Europe, Africa, Australia, and the Americas, despite the fact that the honey bee was not introduced to the Americas until the colonization by Spain and Portugal. They are by far the most common medical insect product both historically and currently, and the most frequently referenced of these is honey.[37] It can be applied to skin to treat excessive scar tissue, rashes, and burns,[38] and as an eye poultice to treat infection.[21] Honey is taken for digestive problems and as a general health restorative. It is taken hot to treat colds, cough, throat infections, laryngitis, tuberculosis, and lung diseases.[34] Apitoxin (honey bee venom) is applied via direct stings to relieve arthritis, rheumatism, polyneuritis, and asthma.[34] Propolis, a resinous, waxy mixture collected by honeybees and used as a hive insulator and sealant, is often consumed by menopausal women because of its high hormone content, and it is said to have antibiotic, anesthetic, and anti-inflammatory properties.[34] Royal jelly is used to treat anaemia, gastrointestinal ulcers, arteriosclerosis, hypo- and hypertension, and inhibition of sexual libido.[34] Finally bee bread, or bee pollen, is eaten as a generally health restorative, and is said to help treat both internal and external infections.[34] One of the major peptides in bee venom, melittin, has the potential to treat inflammation in sufferers of rheumatoid arthritis and multiple sclerosis.[39]

The rise of antibiotic resistant infections has sparked pharmaceutical research for new resources, including into arthropods.[40]

Maggot therapy uses blowfly larvae to perform wound-cleaning debridement.[41]

Cantharidin, the blister-causing oil found in several families of beetles described by the vague common name Spanish fly has been used as an aphrodisiac in some societies.[39]

Blood-feeding insects like ticks, horseflies, and mosquitoes inject multiple bioactive compounds into their prey. These insects have long been used by practitioners of Eastern Medicine to prevent blood clot formation or thrombosis, suggesting possible applications in scientific medicine.[42] Over 1280 protein families have been associated with the saliva of blood feeding organisms, including inhibitors of platelet aggregation, ADP, arachidonic acid, thrombin, PAF, anticoagulants, vasodilators, vasoconstrictors, antihistamines, sodium channel blockers, complement inhibitors, pore formers, inhibitors of angiogenesis, anaesthetics, AMPs and microbial pattern recognition molecules, and parasite enhancers/activators.[39][43][44][45]

In science and technology

Insects play an important role in biological research. Because of its small size, short generation time and high fecundity, the common fruit fly *Drosophila melanogaster* was selected as a model organism for studies of the genetics of higher eukaryotes. *D. melanogaster* has been an essential part of studies into principles like genetic linkage, interactions between genes, chromosomal genetics, evolutionary developmental biology, animal behaviour and evolution. Because genetic systems are well conserved among eukaryotes, understanding basic cellular processes like DNA replication or transcription in fruit flies helps scientists to understand those processes in other eukaryotes, including humans.[46] The genome of *D. melanogaster* was sequenced in 2000, reflecting the fruit fly's important role in biological research. 70% of the fly genome is similar to the human genome, supporting the Darwinian theory of evolution from a single origin of life.[47]



Cochineal scale insects being collected from a prickly pear in Central America. Illustration by José Antonio de Alzate y Ramírez, 1777

Some hemipterans are used to produce dyestuffs such as carmine (also called cochineal). The scale insect *Dactylopius coccus* produces the brilliant red-coloured carminic acid to deter predators. Up to 100,000 scale insects are needed to make a kilogram (2.2 lbs) of cochineal dye.[48][49]



The common fruitfly *Drosophila melanogaster* is one of the most widely used model organisms in biological research.

A similarly enormous number of lac bugs are needed to make a kilogram of shellac, a brush-on colourant and wood finish.[50] Additional uses of this traditional product include the waxing of citrus fruits to extend their shelf-life, and the coating of pills to moisture-proof them, provide slow-release or mask the taste of bitter ingredients.[51]

Kermes is a red dye from the dried bodies of the females of a scale insect in the genus *Kermes*, primarily *Kermes vermilio*. *Kermes* are native to the Mediterranean region, living on the sap of the kermes oak. They were used as a red dye by the ancient Greeks and Romans. The kermes dye is a rich red, and has good colour fastness in silk and wool.[52][53][54][55][56]

Insect attributes are sometimes mimicked in architecture, as at the Eastgate Centre, Harare, which uses passive cooling, storing heat in the morning and releasing it in the warm parts of the day.[57] The target of this piece of biomimicry is the structure of the mounds of termites such as *Macrotermes michaelseni* which effectively cool the nests of these social insects.[58][59] The properties of the Namib desert beetle's exoskeleton, in particular its wing-cases (elytra) which have bumps with hydrophilic (water-attracting) tips and hydrophobic (water-shedding) sides, have been mimicked in a film coating designed for the British Ministry of Defence, to capture water in arid regions.[60][61]



Target for biomimicry research: the Namib desert beetle, *Stenocara gracilipes*, channels water from fog down its wings.

In textiles

Silkworms, the caterpillars and pupae of the moth *Bombyx mori*, have been reared to produce silk in China from the Neolithic Yangshao period onwards, c. 5000 BC.[62][63] Production spread to India by 140 AD.[64] The caterpillars are fed on mulberry leaves. The cocoon, produced after the fourth moult, is covered with a continuous filament of the silk protein, fibroin, gummed together with sericin. In the traditional process, the gum is removed by soaking in hot water, and the silk is then unwound from the cocoon and reeled. Filaments are spun together to make silk thread.[65] Commerce in silk between China and countries to its west began in ancient times, with silk known from an Egyptian mummy of 1070 BC, and later to the ancient Greeks and Romans. The silk road leading west from China was opened in the 2nd century AD, helping to drive trade in silk and other goods.[66]

In warfare

The use of insects for warfare may have been attempted in the Middle Ages or earlier, but was first systematically researched by several nations during the 20th century. It was put into practice by the Japanese army's Unit 731 in attacks on China during the Second World War, killing almost 500,000 Chinese people with fleas infected with plague and flies infected with cholera.[67][68] Also in the Second World War, the Germans explored the use of Colorado beetles to destroy enemy potato crops.[69] During the Cold War, the US Army considered using yellow fever mosquitoes to attack Soviet cities.[67]



Court Ladies Preparing Newly Woven Silk, Song dynasty, 1100–1133

Symbolic uses

In mythology and folklore

Insects have appeared in mythology around the world from ancient times. Among the insect groups featuring in myths are the bee, butterfly, cicada, fly, dragonfly, praying mantis and scarab beetle. Scarab beetles held religious and cultural symbolism in Old Egypt, Greece and some shamanistic Old World cultures. The ancient Chinese regarded cicadas as symbols of rebirth or immortality.[23][70] In the *Homeric Hymn to Aphrodite*, the goddess Aphrodite retells the legend of how Eos, the goddess of the dawn, requested Zeus to let her lover Tithonus live forever as an immortal.[71] Zeus granted her request, but, because Eos forgot to ask him to also make Tithonus ageless, Tithonus never died, but he did grow old.[71] Eventually, he became so tiny and shriveled that he turned into the first cicada.[71]



Gold plaques embossed with winged bee goddesses, perhaps the Thriai, found at Camiros Rhodes, dated to the 7th century BC.

In an ancient Sumerian poem, a fly helps the goddess Inanna when her husband Dumuzid is being chased by *galla* demons.[72] Flies also appear on Old Babylonian seals as symbols of Nergal, the god of death[72] and fly-shaped lapis lazuli beads were often worn by many different cultures in ancient Mesopotamia, along with other kinds of fly-jewellery.[72] The Akkadian *Epic of Gilgamesh* contains allusions to dragonflies, signifying the impossibility of immortality.[23][70]

Amongst the Arrernte Aborigines of Australia, honey ants and witchety grubs served as personal clan totems. In the case of the San bushmen of the Kalahari, it is the praying mantis which holds much cultural significance including creation and zen-like patience in waiting.[23][70]:9



Woolly bear caterpillar larva of the isabella tiger moth, *Pyrrharctia isabella*, is celebrated in the annual Woollybear Festival of the American Great Lakes.

Insects feature in folklore around the world. In China, farmers traditionally regulated their crop planting according to the Awakening of the Insects, when temperature shifts and monsoon rains bring insects out of hibernation. Most "awakening" customs are related to eating snacks like pancakes, parched beans, pears, and fried corn, symbolizing harmful insects in the field.[73]

In the Great Lakes region of the United States, there is an annual Woollybear Festival that has been celebrated for over 40 years. The larvae of the species *Pyrrharctia isabella* (commonly known as the isabella tiger moth), with their 13 distinct segments of black and reddish brown, have the reputation in common folklore of being able to forecast the coming winter weather.[74]

There is a common misconception that cockroaches are serious vectors of disease, but while they can carry bacteria they do not travel far, and have no bite or sting.[75][76] Their shells contain a protein, arylphorin, implicated in asthma and other respiratory conditions.[77]

Many people believe the urban myth that the daddy longlegs (Opiliones) has the most poisonous bite in the spider world, but that the fangs are too small to penetrate human skin. This is untrue on several counts. None of the known species of harvestmen have venom glands; their chelicerae are not hollowed fangs but grasping claws that are typically very small and definitely not strong enough to break human skin.[78][79]

In Japan, the emergence of fireflies and rhinoceros beetles signify the anticipated changing of the seasons.[80]



Shoen Uemura - firefly, a sign of summer in Japan

In religion

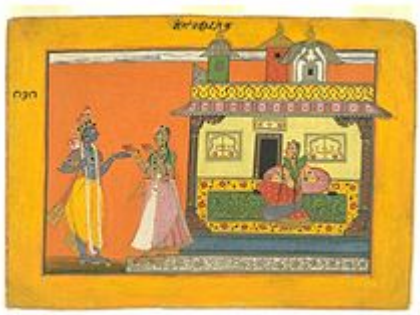
In the Brazilian Amazon, members of the Tupí–Guaraní language family have been observed using *Pachycondyla commutata* ants during female rite-of-passage ceremonies, and prescribing the sting of *Pseudomyrmex* spp. for fevers and headaches.[81]

The red harvester ant *Pogonomyrmex californicus* has been widely used by natives of Southern California and Northern Mexico for hundreds of years in ceremonies conducted to help tribe members acquire spirit helpers through hallucination. During the ritual, young men are sent away from the tribe and consume large quantities of live, unmasticated ants under the supervision of an elderly member of the tribe. Ingestion of ants should lead to a prolonged state of unconsciousness, where dream helpers appear and serve as allies to the dreamer for the rest of his life.[82]



Scarab with separate wings, c. 712-342 BC.

In art



Radha and Krishna in Rasamanjari by Bhanudatta, Basohli, c. 1670. Opaque watercolour and gold on paper, with applied beetlewing fragments

Both the symbolic form and the actual body of insects have been used to adorn humans in ancient and modern times. A recurrent theme for ancient cultures in Europe and the Near East regarded the sacred image of a bee or human with insect features. Often referred to as the bee "goddess", these images were found in gems and stones. An onyx gem from Knossos (ancient Crete) dating to approximately 1500 BC illustrates a Bee goddess with bull horns above her head. In this instance, the figure is surrounded by dogs with wings, most likely representing Hecate and Artemis – gods of the underworld, similar to the Egyptian gods Akeu and Anubis.[83]

Beetlewing art is an ancient craft technique using iridescent beetle wings practiced traditionally in Thailand, Myanmar, India, China and Japan. Beetlewing pieces are used as an adornment to paintings, textiles and jewelry. Different species of metallic wood-boring beetle wings were used depending on the region, but traditionally the most valued were those from beetles belonging to the genus Sternocera. The practice comes from across Asia and Southeast Asia, especially Thailand, Myanmar, Japan, India and China. In Thailand beetlewings were preferred to decorate clothing (shawls and Sabai cloth) and jewellery in former court circles.[84]

The Canadian entomologist Charles Howard Curran's 1945 book, *Insects of the Pacific World*, noted women from India and Sri Lanka, who kept $1\frac{1}{2}$ inch (38 mm) long, iridescent greenish coppery beetles of the species *Chrysochroa ocellata* as pets. These living jewels were worn on festive occasions, probably with a small chain attached to one leg anchored to the clothing to prevent escape. Afterwards, the insects were bathed, fed, and housed in decorative cages. Living jewelled beetles have also been worn and kept as pets in Mexico.[85]



A Dragon-fly, Two Moths, a Spider and Some Beetles, With Wild Strawberries by Jan van Kessel, 17th century. Wasp beetle, top left; clouded border moth, top right; migrant hawker dragonfly and cardinal beetle, centre left; magpie moth, centre right; cockchafer, lower left.

Butterflies have long inspired humans with their life cycle, color, and ornate patterns. The novelist Vladimir Nabokov was also a renowned butterfly expert. He published and illustrated many butterfly species, stating:

> I discovered in nature the nonutilitarian delights that I sought in art. Both were a form of magic, both were games of intricate enchantment and deception.[86]

It was the aesthetic complexity of insects that led Nabokov to reject natural selection.[87][88]

The naturalist Ian MacRae writes of butterflies:

> the animal is at once awkward, flimsy, strange, bouncy in flight, yet beautiful and immensely sympathetic; it is painfully transient, albeit capable of extreme migrations and transformations. Images and phrases such as "kaleidoscopic instabilities," "oxymoron of similarities," "rebellious rainbows," "visible darkness" and "souls of stone" have much in common. They bring together the two terms of a conceptual contradiction, thereby facilitating the mixing of what should be discrete and mutually exclusive categories ... In positing such questions, butterfly science, an inexhaustible, complex, and finely nuanced field, becomes not unlike the human imagination, or the field of literature itself. In the natural history of the animal, we begin to sense its literary and artistic possibilities.[89]

The photographer Kjell Sandved spent 25 years documenting all 26 characters of the Latin alphabet using the wing patterns of butterflies and moths as *The Butterfly Alphabet*.[90]

In 2011, the artist Anna Collette created over 10,000 individual ceramic insects at Nottingham Castle, "Stirring the Swarm". Reviews of the exhibit offered a compelling narrative for cultural entomology: "the unexpected use of materials, dark overtones, and the straightforward impact of thousands of tiny multiples within the space. The exhibition was at once both exquisitely beautiful and deeply repulsive, and this strange duality was fascinating."[91][92]

In literature and film

The Ancient Greek playwright Aeschylus has a gadfly pursue and torment Io, a maiden associated with the moon, watched constantly by the eyes of the herdsman Argus, associated with all the stars: "Io: Ah! Hah! Again the prick, the stab of gadfly-sting! O earth, earth, hide, the hollow shape—Argus—that evil thing—the hundred-eyed." William Shakespeare, inspired by Aeschylus, has Tom o'Bedlam in *King Lear*, "Whom the foul fiend hath led through fire and through flame, through ford and whirlpool, o'er bog and quagmire", driven mad by the constant pursuit.[93] In *Antony and Cleopatra*, Shakespeare similarly likens Cleopatra's hasty departure from the Actium battlefield to that of a cow chased by a gadfly.[94] H. G. Wells introduced giant wasps in his 1904 novel *The Food of the Gods and How It Came to Earth*,[95] making use of the newly discovered growth hormones to lend plausibility to his science fiction.[96] Lafcadio Hearn's essay *Butterflies* analyses the treatment of the butterfly

in Japanese literature, both prose and poetry. He notes that these often allude to Chinese tales, such as of the young woman that the butterflies took to be a flower. He translates 22 Japanese haiku poems about butterflies, including one by the haiku master Matsuo Bashō, said to suggest happiness in springtime: "Wake up! Wake up!—I will make thee my comrade, thou sleeping butterfly."[97]

The novelist Vladimir Nabokov was the son of a professional lepidopterist, and was interested in butterflies himself.[98] He wrote his novel *Lolita* while travelling on his annual butterfly-collection trips in the western United States.[99] He eventually became a leading lepidopterist. This is reflected in his fiction, where for example *The Gift* devotes two whole chapters (of five) to the tale of a father and son on a butterfly expedition.[100]

Horror films involving insects, sometimes called "big bug movies", include the pioneering 1954 *Them!*, featuring giant ants mutated by radiation, and the 1957 *The Deadly Mantis*.[101][102][103]



Poster for the 1957 film *The Deadly Mantis*

The Far Side, a newspaper cartoon, has been used by professor of Michael Burgett as a teaching tool in his entomology class; *The Far Side* and its author Gary Larson have been acknowledged by biologist Dale H. Clayton his colleague for "the enormous contribution" Larson has made to their field through his cartoons.[104][105]

In music

The "Flight of the Bumblebee" was written by Nikolai Rimsky-Korsakov, in 1899–1900, as part of his opera, *The Tale of Tsar Saltan*. The piece is one of the most recognizable pieces in classical composition. The bumblebee in the story is a prince who has been transformed into an insect so that he can fly off to visit his father.[106][107][108] The play upon which the opera was based – written by Alexandr Pushkin – originally had two more insect themes: the Flight of the Mosquito and the Flight of the Fly.[109]

The Hungarian composer Béla Bartók explained in his diary that he was attempting to depict the desperate attempts to escape of a fly caught in a cobweb in his piece *From the Diary of a Fly, for piano (Mikrokosmos Vol. 6/142)*.[110]

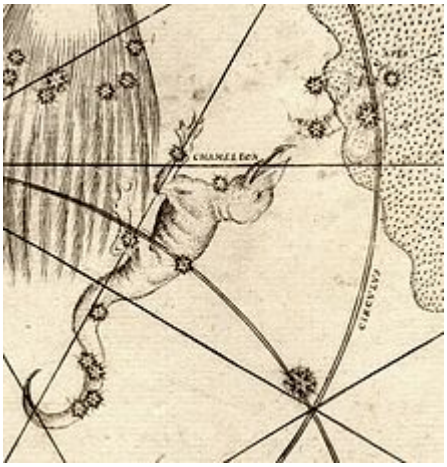
The jazz musician and philosophy professor David Rothenberg plays duets with singing insects including cicadas, crickets, and beetles.[111]

In astronomy and cosmology

In astronomy, constellations named after arthropods include the zodiacal Scorpius, the scorpion,[112][113] and Musca, the fly, also known as Apis, the bee, in the deep southern sky. Musca, the only recognised insect constellation, was named by Petrus Plancius in 1597.[114]

"The Bug Nebula", also called "The Butterfly Nebula", is a more recent discovery. Known as NGC 6302 is one of the brightest and most popular stars in the universe – popular in that its features draw the attention of a lot of researchers. It happens to be located in the Scorpius constellation. It is perfectly bipolar, and until recently, the central star was unobservable, clouded by gas, but estimated to be one of the hottest in the galaxy – 200,000 degrees Fahrenheit, perhaps 35 times hotter than our Sun.[115][116]

The honey bee played a central role in the cosmology of the Mayan people. The stucco figure at the temples of Tulum known as "Ah Mucen Kab" – the Diving Bee God – bears resemblance to the insect in the Codex Tro-Cortesianus identified as a bee. Such reliefs might have indicated towns and villages that produce honey. Modern Mayan authorities say the figure also have a connection to modern cosmology. Mayan mythology expert Migel Angel Vergara relates that the Mayans held a belief that bees came from Venus, the "Second Sun." The relief might be indicative of another "insect deity", that of Xux Ex, the Mayan "wasp



The constellation Musca (as Apis) is upper right. Detail from Johann Bayer's *Uranometria*, 1603

star."[117] The Mayan embodied Venus in the form of the god Kukulkán (also known as or related to Gukumatz and Quetzalcoatl in other parts of Mexico), Quetzalcoatl is a Mesoamerican deity whose name in Nahuatl means "feathered serpent". The cult was the first Mesoamerican religion to transcend the old Classic Period linguistic and ethnic divisions. This cult facilitated communication and peaceful trade among peoples of many different social and ethnic backgrounds.[118] Although the cult was originally centered on the ancient city of Chichén Itzá in the modern Mexican state of Yucatán, it spread as far as the Guatemalan highlands.[119]



The Butterfly Nebula, NGC 6302

In costumes

Bee and other insect costumes are worn in a variety of countries for parties, carnivals and other celebrations.[120][121]



A bee costume for a Mardi Gras celebration

Ovo is an insect-themed production by the world renowned Canadian entertainment company Cirque du Soleil. The show looks at the world of insects and its biodiversity where they go about their daily lives until a mysterious egg appears in their midst, as the insects become awestruck about this iconic object that represents the enigma and cycles of their lives. The costuming was a fusion of arthropod body types blended with superhero armour. Liz Vandal, the lead costume designer, has a special affinity for the world of the insect:[122]

> When I was just a kid I put rocks down around the yard near the fruit trees and I lifted them regularly to watch the insects who had taken up residence underneath them. I petted caterpillars and let butterflies into the house. So when I learned that OVO was inspired by insects, I immediately knew that I was in a perfect position to pay tribute to this majestic world with my costumes. All insects are beautiful and perfect; it is what they evoke for each of us that changes our perception of them."[122]

The Webby award-winning video series *Green Porno* was created to showcase the reproductive habits of insects. Jody Shapiro and Rick Gilbert were responsible for translating the research and concepts that Isabella Rossellini envisioned into the paper and paste costumes which directly contribute to the series' unique visual style. The film series was driven by the creation of costumes to translate scientific research into "something visual and how to make it comical."[123]

See also

- Arthropods in culture
- Birds in culture
- Plants in culture

Arthropods in culture

Culture consists of the social behaviour and norms in human societies transmitted through social learning.[1] Arthropods play many roles in human culture, including as food, in art, in stories, and in mythology and religion. Many of these concern insects, which are important both economically and symbolically, from the work of honeybees to the scarabs of Ancient Egypt. Other arthropods with cultural significance include crustaceans such as crabs, lobsters, and crayfish, which are popular subjects in art, especially still lifes, and arachnids such as spiders and scorpions, whose venom has medical applications. The crab and the scorpion are astrological signs of the zodiac.



Crayfish and Two Shrimps by Utagawa Hiroshige, 1835-1845

Contents

Overview
As food
In science and engineering
In medicine
In folklore, mythology and religion
In art, literature, and music
References

Overview

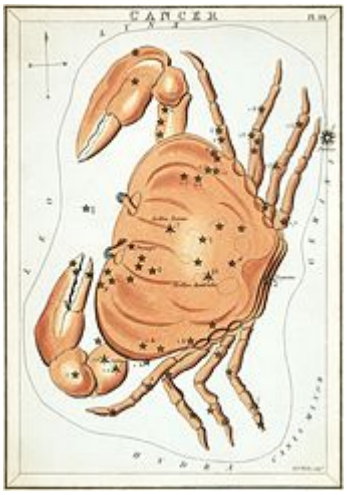
Culture consists of the social behaviour and norms found in human societies and transmitted through social learning. Cultural universals in all human societies include expressive forms like art, music, dance, ritual, religion, and technologies like tool usage, cooking, shelter, and clothing. The concept of material culture covers physical expressions such as technology, architecture and art, whereas immaterial culture includes principles of social organization, mythology, philosophy, literature, and science.[1] This article describes the roles played by arthropods in human culture.



Gold plaques embossed with winged bee goddesses, perhaps the Thriai, found at Camiros Rhodes, dated to the 7th century B.C.

The arthropods are a phylum of animals with jointed legs; they include the insects, arachnids such as spiders, myriapods, and crustaceans.[2] Insects play many roles in culture including their direct use as food,[3] in medicine,[4] for dyestuffs,[5] and in science, where the common fruit fly *Drosophila melanogaster* serves as a model organism for work in genetics and developmental biology.[6]

As food



The constellation of Cancer, the crab, from Urania's Mirror, c. 1825

Crustaceans are an important source of food, providing nearly 10,700,000 tons in 2007; the vast majority of this output is of decapods: crabs, lobsters, shrimps, crayfish, and prawns. Over 60% by weight of all crustaceans caught for consumption are shrimp and prawns, and nearly 80% is produced in Asia, with China alone producing nearly half the world's total. Non-decapod crustaceans are not widely consumed, with only 118,000 tons of krill being caught, despite krill having one of the greatest biomasses on the planet.[7][8]

Crabs make up 20% of all marine crustaceans caught, farmed, and consumed worldwide, amounting to 1.5 million tonnes annually. One species, *Portunus trituberculatus*, accounts for one-fifth of that total. Other commercially important taxa include *Portunus pelagicus*, several species in the genus *Chionoecetes*, the blue crab (*Callinectes sapidus*), *Charybdis* spp., *Cancer pagurus*, the Dungeness crab (*Metacarcinus magister*), and *Scylla serrata*, each of which yields more than 20,000 tonnes annually.[9]

Lobsters are caught using baited, one-way traps with a colour-coded marker buoy to mark cages. Lobster is fished in water between 2 and 900 metres (1 and 500 fathoms), although some lobsters live at 3,700 metres (2,000 fathoms). Cages are of plastic-coated galvanised steel or wood. A lobster fisher may tend as many as 2,000 traps. Around 2000, owing to overfishing and high demand, lobster aquaculture expanded.[10] As of 2008, no lobster aquaculture operation had achieved commercial success, mainly because lobsters eat each other (cannibalism) and the growth of the species is slow.[11]

Spiders are sometimes used as food. Cooked tarantula spiders are considered a delicacy in Cambodia,[12] and by the Piaroa Indians of southern Venezuela – provided the highly irritant hairs, the spiders' main defence system, are removed first.[13]


Cooked tarantula spiders are a delicacy in Cambodia.

In science and engineering

Insects feature in a variety of ways in biomimicry, where for example the cooling system of termite mounds has been imitated in architecture.[14]

Spider venoms may be a less polluting alternative to conventional pesticides, as they are deadly to insects but the great majority are harmless to vertebrates. Australian funnel web spiders are a promising source, as most of the world's insect pests have had no opportunity to develop any immunity to their venom, and funnel web spiders thrive in captivity and are easy to "milk". It may be possible to target specific pests by engineering genes for the production of spider toxins into viruses that infect species such as cotton bollworms.[15]

Because spider silk is both light and strong, attempts are being made to produce it in goats' milk and in the leaves of plants, by means of genetic engineering.[16][17]

In medicine

The Ch'ol Maya use a beverage created from the tarantula *Brachypelma vagans* for a condition they term 'tarantula wind', the symptoms of which include chest pain, asthma and coughing. The peptide GsMtx-4, found in the venom, has been studied for possible use in cardiac arrhythmia, muscular dystrophy, and glioma.[18] Possible medical uses for other spider venoms have been investigated for the treatment of cardiac arrhythmia,[19] Alzheimer's disease,[20] strokes,[21] and erectile dysfunction.[22]

In folklore, mythology and religion



Moche ceramic spider, c. 300 AD

Arthropods appear in folklore, in mythology,[23] and in religion.[24] Since Insects in mythology and in religion are covered elsewhere, this section focuses on other arthropods.

Both the constellation Cancer and the astrological sign Cancer are named after the crab, and depicted as a crab. William Parsons, 3rd Earl of Rosse drew the Crab Nebula in 1848 and noticed its similarity to the animal; the Crab pulsar lies at the centre of the nebula.[25] The Moche people of ancient Peru worshipped nature, especially the sea,[26] and often depicted crabs in their art.[27] In Greek mythology, Karkinos was a crab that came to the aid of the Lernaean Hydra as it battled Heracles. One of Rudyard Kipling's *Just So Stories*, *The Crab that Played with the Sea*, tells the story of a gigantic crab who made the waters of the sea go up and down, like the tides.[28]

In the Japanese fairy tale "My Lord Bag of Rice", the warrior Fujiwara no Hidesato slays a giant centipede, Ōmukade, to help a dragon princess.[29]

Spiders have been depicted in stories, mythologies and the arts of many cultures for centuries.[30] They have symbolized patience due to their hunting technique of setting webs and waiting for prey, as well as mischief and malice due to their venomous bites.[31] The Italian tarantella is a dance supposedly to rid the young woman of the lustful effects of a bite by the tarantula wolf spider, *Lycosa tarantula*.[32] Web-spinning caused the association of the spider with creation myths, as they seem to produce their own worlds.[33] Dreamcatchers are depictions of spiderwebs. The Moche people of ancient Peru worshipped nature,[34] emphasising animals and often depicting spiders in their art.[35]



Scorpion motif is often woven into Turkish kilim flatweave carpets, for protection from their sting (2 examples).

The scorpion appeared as the astrological sign *Scorpio*, in the twelve signs of the Zodiac, created by Babylonian astronomers during the Chaldean period, around 600 BC.[36] In South Africa and South Asia, the scorpion is a significant animal culturally, appearing as a motif in art, especially in Islamic art in the Middle East.[37] A scorpion motif is often woven into Turkish kilim flatweave carpets, for protection from their sting.[38] The scorpion is perceived both as an embodiment of evil and a protective force that counters evil, such as a dervish's powers to combat evil.[37] In another context, the scorpion portrays human sexuality.[37] Scorpions are used in folk medicine in South Asia especially in antidotes for scorpion stings.[37] In ancient Egypt the goddess Serket was often depicted as a scorpion, one of several goddesses who protected the Pharaoh.[39]

In art, literature, and music

Insects feature in art,[40] in literature, in film,[41] and in music.

The "Lobster Quadrille", also known as "The Mock Turtle's Song", is a song recited by the Mock Turtle in *Alice's Adventures in Wonderland*, chapters 9 and 10, accompanied by a dance.[42]

The surrealist artist Salvador Dali created a sculpture called *Lobster Telephone* with the crustacean in place of the traditional handset, resting in the cradle above the dial.[43] The Surrealist filmmaker Luis Buñuel used scorpions in his 1930 classic *L'Age d'or* (*The Golden Age*).[44]



Lewis Carroll's lobster, drawn by Sir John Tenniel, 1869



Crustaceans in Roman mosaic in the 'House of the Dancing Faun', Pompeii (by 79 AD)



Still Life with Crab, Shrimps and Lobster, Clara Peeters, c. 1600



Pronk *Still life with lobster*, Jasper Geeraerts, 1650–1654



Le Crabe by William-Adolphe Bouguereau, 1869



The Lobster by Samuel Peploe, c. 1903



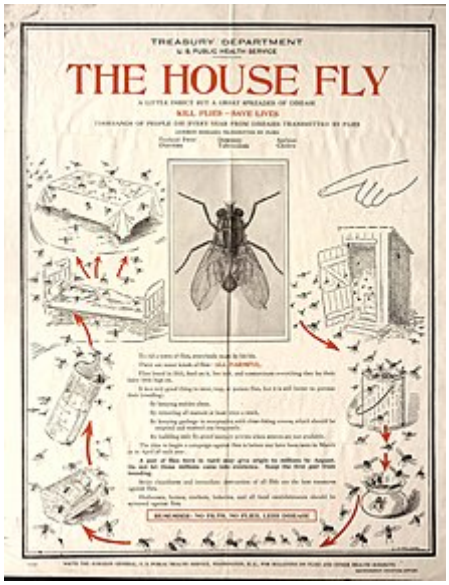
Illustration from *The Water-Babies* by Charles Kingsley, illustrated by Warwick Goble (d. 1943)

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List of common household pests

This is a **list of common household pests** – undesired animals that have a history of living, invading, causing damage, eating human foods, acting as disease vectors or causing other harms in human habitation.



The house fly is found all over the world where humans live and so is the most widely distributed insect.[1]

Contents

Mammals

Invertebrates

See also

References

Mammals

- Mice
 - Field mice
 - House mice
- Rats
 - Black rats
 - Brown rats
 - Wood rats
 - Cotton rats

Invertebrates

- Ants
 - Argentine ants
 - Carpenter ants
 - Fire ants
 - Odorous house ants
 - Pharaoh ants
 - Thief ants
- Bed bugs[2]
- Beetles
 - Woodworms
 - Death watch beetles
 - Furniture beetles
 - Weevils
 - Maize weevil
 - Rice weevil
 - Carpet beetles

 - Fur beetles
 - Varied carpet beetles
 - Spider beetles
 - Mealworm beetles
- Centipedes
 - House centipedes
- Cockroaches
 - Brown-banded cockroaches
 - German cockroaches
 - American cockroaches
 - Oriental cockroaches
- Dust mites[3]
- Earwigs
- Crickets
 - House crickets
- Flies
 - Bottle flies
 - Blue bottle flies
 - Green bottle flies
 - House flies[1]
 - Fruit flies
- Mosquitoes
- Moths
 - Almond moths
 - Indianmeal moths
 - Clothes moths
 - Gypsy moths
 - Common clothes moths
 - Brown house moths
- Paper Lice
- Red spiders
- Silverfish
- Woodlice
- Termites[4]
 - Dampwood termites
 - Subterranean termites

See also

- Home-stored product entomology
- List of notifiable diseases
- Noxious weed
- Pest (organism)

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Ant

Ants are eusocial insects of the family **Formicidae** and, along with the related wasps and bees, belong to the order Hymenoptera. Ants evolved from wasp-like ancestors in the Cretaceous period, about 140 million years ago, and diversified after the rise of flowering plants. More than 12,500 of an estimated total of 22,000 species have been classified.[5][6] They are easily identified by their elbowed antennae and the distinctive node-like structure that forms their slender waists.

Ants form colonies that range in size from a few dozen predatory individuals living in small natural cavities to highly organised colonies that may occupy large territories and consist of millions of individuals. Larger colonies consist of various castes of sterile, wingless females, most of which are workers (ergates), as well as soldiers (dinergates) and other specialised groups.[7][8] Nearly all ant colonies also have some fertile males called "drones" (aner) and one or more fertile females called "queens" (gynes).[8] The colonies are described as superorganisms because the ants appear to operate as a unified entity, collectively working together to support the colony.[9][10]

Ants have colonised almost every landmass on Earth. The only places lacking indigenous ants are Antarctica and a few remote or inhospitable islands. Ants thrive in most ecosystems and may form 15–25% of the terrestrial animal biomass.[11] Their success in so many environments has been attributed to their social organisation and their ability to modify habitats, tap resources, and defend themselves. Their long co-evolution with other species has led to mimetic, commensal, parasitic, and mutualistic relationships.[12]

Ant societies have division of labour, communication between individuals, and an ability to solve complex problems.[13] These parallels with human societies have long been an inspiration and subject of study. Many human cultures make use of ants in cuisine, medication, and rituals. Some species are valued in their role as biological pest control agents.[14] Their ability to exploit resources may bring ants into conflict with humans, however, as they can damage crops and invade buildings. Some species, such as the red imported fire ant (*Solenopsis invicta*), are regarded as invasive species, establishing themselves in areas where they have been introduced accidentally.[15]

Contents

Etymology

Taxonomy and evolution

Ants

Temporal range: 140–0 Ma[1]

PreЄ Є O S D C P T J K PgN

Berriasian – Present



A group of fire ants.

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Superfamily:	Formicoidea
Family:	Formicidae Latreille, 1809

Type species

Formica rufa
Linnaeus, 1761

Subfamilies

Distribution and diversity

Morphology
- Head
- Mesosoma
- Metasoma
- Polymorphism

Life cycle
- Reproduction

Behaviour and ecology
- Communication
- Defence
- Learning
- Nest construction
- Cultivation of food
- Navigation
- Locomotion
- Cooperation and competition
- Relationships with other organisms

Relationship with humans
- As food
- As pests
- In science and technology
- As pets
- In culture

See also

References
- Cited texts

Further reading

External links

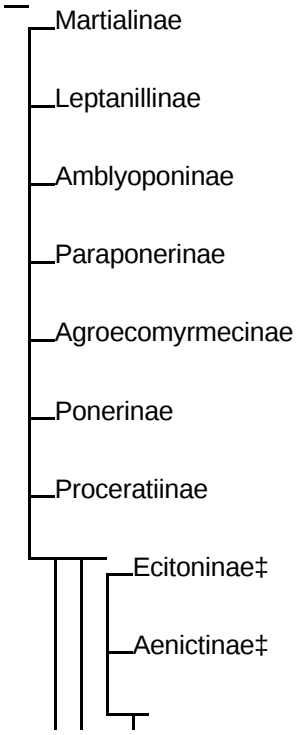
Etymology

The word *ant* and its chiefly dialectal form *emmet*[16] come from *ante*, *emete* of Middle English, which come from *æmette* of Old English, and these are all related to the dialectal Dutch *emt* and the Old High German *āmeiza*, from which comes the modern German *Ameise*. All of these words come from West Germanic **æmaitjōn*, and the original meaning of the word was "the biter" (from Proto-Germanic **ai-*, "off, away" + **mait-* "cut").[17][18] The family name Formicidae is derived from the Latin *formīca* ("ant")[19] from which the words in other Romance languages, such as the Portuguese *formiga*, Italian *formica*, Spanish *hormiga*, Romanian *furnică*, and French *fourmi* are derived. It has been hypothesised that a Proto-Indo-European word *morwi- was used, cf. Sanskrit vamrah, Latin formīca, Greek μύρμηξ *mýrmēx*, Old Church Slavonic *mraviji*, Old Irish *moirb*, Old Norse *maurr*, Dutch *mier*.[20]

Taxonomy and evolution

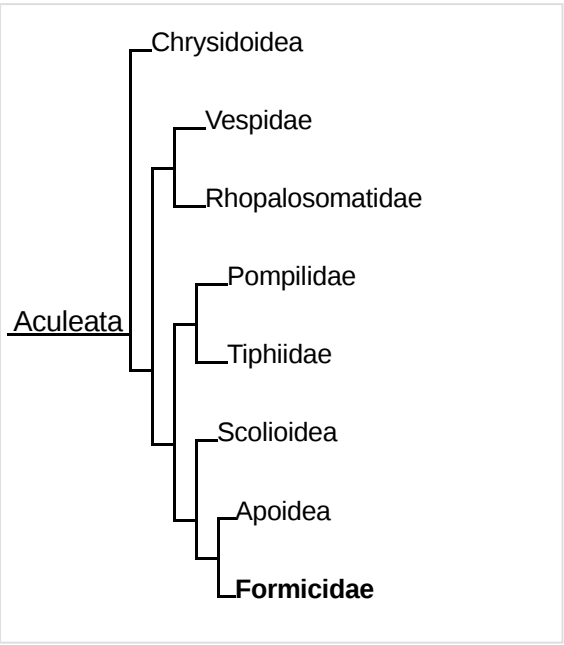
- Agroecomyrmecinae
- Amblyoponinae (incl. "Apomyrminae")
- Aneuretinae
- †Brownimeciinae
- Dolichoderinae
- Dorylinae
- Ectatomminae
- †Formiciinae
- Formicinae
- Heteroponerinae
- Leptanillinae
- Martialinae
- Myrmeciinae (incl. "Nothomyrmeciinae")
- Myrmicinae
- Paraponerinae
- Ponerinae
- Proceratiinae
- Pseudomyrmecinae
- †Sphecomyrminae

Cladogram of subfamilies

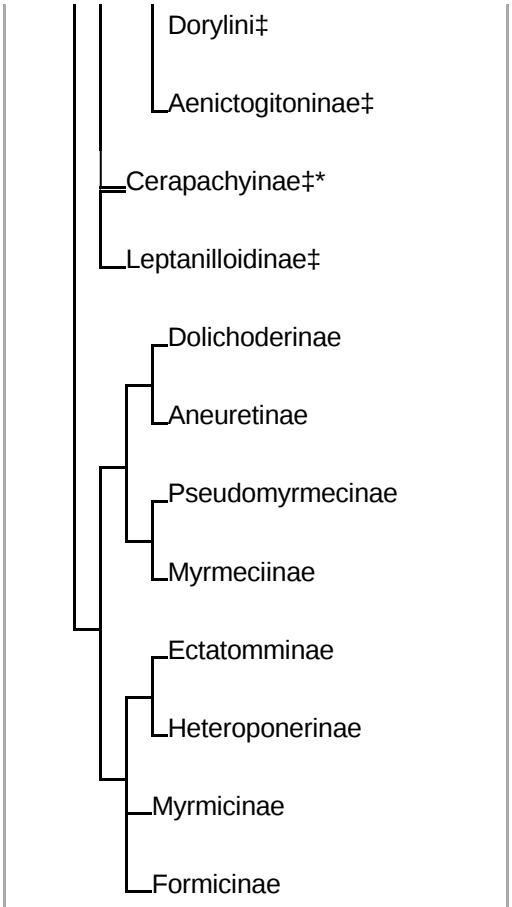


The family Formicidae belongs to the order Hymenoptera, which also includes sawflies, bees, and wasps. Ants evolved from a lineage within the stinging wasps, and a 2013 study suggests that they are a sister group of the Apoidea.[21] In 1966, E. O. Wilson and his colleagues identified the fossil remains of an ant (*Sphecomyrma*) that lived in the Cretaceous period. The specimen, trapped in amber dating back to around 92 million years ago, has features found in some wasps, but not found in modern ants.[22] *Sphecomyrma* was possibly a ground forager, while *Haidomyrmex* and *Haidomyrmodes*, related genera in subfamily Sphecomyrminae, are reconstructed as active arboreal predators.[23] Older ants in the genus *Sphecomyrmodes* have been found in 99 million year-old amber from Myanmar.[24][25] A 2006 study suggested that ants arose tens of millions of years earlier than previously thought, up to 168 million years ago.[1] After the rise of flowering plants about 100 million years ago they diversified and assumed ecological dominance around 60 million years ago.[26][1][27][28] Some groups, such as the Leptanillinae and Martialinae, are suggested to have diversified from early primitive ants that were likely to have been predators underneath the surface of the soil.[3][29]

During the Cretaceous period, a few species of primitive ants ranged widely on the Laurasian supercontinent (the Northern Hemisphere). They were scarce in comparison to the populations of other insects, representing only about 1% of the entire insect population. Ants became dominant after adaptive radiation at the beginning of the Paleogene period. By the Oligocene and Miocene, ants had come to represent 20–40% of all insects found in major fossil deposits. Of the species that lived in the Eocene epoch, around one in 10 genera survive to the present. Genera surviving today comprise 56% of the genera in Baltic amber fossils (early Oligocene), and 92% of the genera in Dominican amber fossils (apparently early Miocene).[26][30]



Phylogenetic position of the Formicidae.[21]



A phylogeny of the extant ant subfamilies.[2][3]
*Cerapachyinae is paraphyletic
‡ The previous dorylomorph subfamilies were synonymized under Dorylinae by Brady *et al.* in 2014[4]


Play media
(video) Ants gathering food

Termites live in colonies and are sometimes called ‘white ants’, but termites are not ants. They are the sub-order Isoptera, and together with cockroaches they form the order Blattodea. Blattodeans are related to mantids, crickets, and other winged insects that do not undergo full metamorphosis. Like ants, termites are eusocial, with sterile workers, but they differ greatly in the genetics of reproduction. The similarity of their social structure to that of ants is attributed to convergent evolution.[31] Velvet ants look like large ants, but are wingless female wasps.[32][33]

Distribution and diversity



Ants fossilised in Baltic amber

Ants are found on all continents except Antarctica, and only a few large islands, such as Greenland, Iceland, parts of Polynesia and the Hawaiian Islands lack native ant species.[35][36] Ants occupy a wide range of ecological niches and exploit many different food resources as direct or indirect herbivores, predators and scavengers. Most ant species are omnivorous generalists, but a few are specialist feeders. Their ecological dominance is demonstrated by their biomass: ants are estimated to contribute 15–20 % (on average and nearly 25% in the tropics) of terrestrial animal biomass, exceeding that of the vertebrates.[11]

Region	Number of species [34]
Neotropics	2,162
Nearctic	580
Europe	180
Africa	2,500
Asia	2,080
Melanesia	275
Australia	985
Polynesia	42

Ants range in size from 0.75 to 52 millimetres (0.030–2.0 in),[37][38] the largest species being the fossil *Titanomyrma giganteum*, the queen of which was 6 centimetres (2.4 in) long with a wingspan of 15 centimetres (5.9 in).[39] Ants vary in colour; most ants are red or black, but a few species are green and some tropical species have a metallic lustre. More than 12,000 species are currently known (with upper estimates of the potential existence of about 22,000) (see the article List of ant genera), with the greatest diversity in the tropics. Taxonomic studies continue to resolve the classification and systematics of ants. Online databases of ant species, including AntBase (http://antbase.org/) and the Hymenoptera Name Server (https://hns.osu.edu/), help to keep track of the known and newly described species.[40] The relative ease with which ants may be sampled and studied in ecosystems has made them useful as indicator species in biodiversity studies.[41][42]

Morphology

Ants are distinct in their morphology from other insects in having elbowed antennae, metapleural glands, and a strong constriction of their second abdominal segment into a node-like petiole. The head, mesosoma, and metasoma are the three distinct body segments (formally tagmata). The petiole forms a narrow waist between their mesosoma (thorax plus the first abdominal segment, which is fused to it) and gaster (abdomen less the abdominal segments in the petiole). The petiole may be formed by one or two nodes (the second alone, or the second and third abdominal segments).[43]

Like other insects, ants have an exoskeleton, an external covering that provides a protective casing around the body and a point of attachment for muscles, in contrast to the internal skeletons of humans and other vertebrates. Insects do not have lungs; oxygen and other gases, such as carbon dioxide, pass through their exoskeleton via tiny valves called spiracles. Insects also lack closed blood vessels; instead, they have a long, thin, perforated tube along the top of the body (called the "dorsal aorta") that functions like a heart, and pumps haemolymph toward the head, thus driving the circulation of the internal fluids. The nervous system consists of a ventral nerve cord that runs the length of the body, with several ganglia and branches along the way reaching into the extremities of the appendages.[44]

Head

An ant's head contains many sensory organs. Like most insects, ants have compound eyes made from numerous tiny lenses attached together. Ant eyes are good for acute movement detection, but do not offer a high resolution image. They also have three small ocelli (simple eyes) on the top of the head that detect light levels and polarization.[45] Compared to vertebrates, most ants have poor-to-mediocre eyesight and a few subterranean species are completely blind. However, some ants, such as Australia's

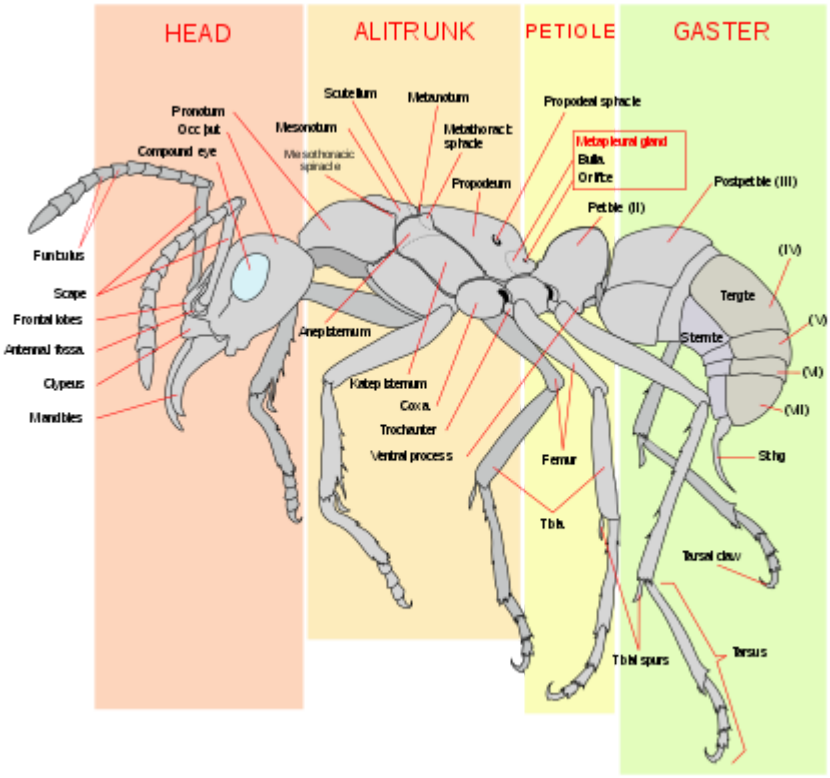


Diagram of a worker ant (*Pachycondyla verenae*)

bulldog ant, have excellent vision and are capable of discriminating the distance and size of objects moving nearly a metre away.[46]

Two antennae ("feelers") are attached to the head; these organs detect chemicals, air currents, and vibrations; they also are used to transmit and receive signals through touch. The head has two strong jaws, the mandibles, used to carry food, manipulate objects, construct nests, and for defence.[44] In some species, a small pocket (infrabuccal chamber) inside the mouth stores food, so it may be passed to other ants or their larvae.[47]

Mesosoma

Both the legs and wings of the ant are attached to the mesosoma ("thorax"). The legs terminate in a hooked claw which allows them to hook on and climb surfaces.[48] Only reproductive ants, queens, and males, have wings. Queens shed their wings after the nuptial flight, leaving visible stubs, a distinguishing feature of queens. In a few species, wingless queens (ergatoids) and males occur.[44]



Macro portrait of an ant

Metasoma

The metasoma (the "abdomen") of the ant houses important internal organs, including those of the reproductive, respiratory (tracheae), and excretory systems. Workers of many species have their egg-laying structures modified into stings that are used for subduing prey and defending their nests.[44]



Bull ant showing the powerful mandibles and the relatively large compound eyes that provide excellent vision

Polymorphism

In the colonies of a few ant species, there are physical castes—workers in distinct size-classes, called minor, median, and major ergates. Often, the larger ants have disproportionately larger heads, and correspondingly stronger mandibles. These are known as macrergates while smaller workers are known as micrergates.[8] Although formally known as dinergates, such individuals are sometimes called "soldier" ants because their stronger mandibles make them more effective in fighting, although they still are workers and their "duties" typically do not vary greatly from the minor or median workers. In a few species, the median workers are absent, creating a sharp divide between the minors and majors.[49] Weaver ants, for example,

have a distinct bimodal size distribution.[50][51] Some other species show continuous variation in the size of workers. The smallest and largest workers in *Pheidologeton diversus* show nearly a 500-fold difference in their dry-weights.[52]



Seven leafcutter ant workers of various castes (left) and two queens (right)

Workers cannot mate; however, because of the haplodiploid sex-determination system in ants, workers of a number of species can lay unfertilised eggs that become fully fertile, haploid males. The role of workers may change with their age and in some species, such as honeypot ants, young workers are fed until their gasters are distended, and act as living food storage vessels. These food storage workers are called *repletes*.[53] For instance, these replete workers develop in the North American honeypot ant *Myrmecocystus mexicanus*. Usually the largest workers in the colony develop into repletes; and, if repletes are removed from the colony, other workers become repletes, demonstrating the flexibility of this particular polymorphism.[54] This polymorphism in morphology and behaviour of workers initially was thought to be determined by environmental factors such as nutrition and hormones that led to different developmental paths; however, genetic differences between worker castes have been noted in *Acromyrmex* sp.[55] These polymorphisms are caused by relatively small genetic changes; differences in a single gene of *Solenopsis invicta* can decide whether the colony will have single or multiple queens.[56] The Australian jack jumper ant (*Myrmecia pilosula*) has only a single pair of chromosomes (with the males having just one chromosome as they are haploid), the lowest number known for any animal, making it an interesting subject for studies in the genetics and developmental biology of social insects.[57][58]

Life cycle

The life of an ant starts from an egg. If the egg is fertilised, the progeny will be female diploid; if not, it will be male haploid. Ants develop by complete metamorphosis with the larva stages passing through a pupal stage before emerging as an adult. The larva is largely immobile and is fed and cared for by workers. Food is given to the larvae by trophallaxis, a process in which an ant regurgitates liquid food held in its crop. This is also how adults share food, stored in the "social stomach". Larvae, especially in the later stages, may also be provided solid food, such as trophic eggs, pieces of prey, and seeds brought by workers.



Meat eater ant nest during swarming

The larvae grow through a series of four or five moults and enter the pupal stage.
The pupa has the appendages free and not fused to the body as in a butterfly pupa.[59] The differentiation into queens and workers (which are both female), and different castes of workers, is influenced in some species by the nutrition the larvae obtain. Genetic influences and the control of gene expression by the developmental environment are complex and the determination of caste continues to be a subject of research.[60] Winged male ants, called drones, emerge from pupae along with the usually winged breeding females. Some species, such as army ants, have wingless queens. Larvae and pupae need to be kept at fairly constant temperatures to ensure proper development, and so often, are moved around among the various brood chambers within the colony.[61]

A new ergate spends the first few days of its adult life caring for the queen and young. She then graduates to digging and other nest work, and later to defending the nest and foraging. These changes are sometimes fairly sudden, and define what are called temporal castes. An explanation for the sequence is suggested by the high casualties involved in foraging, making it an acceptable risk only for ants who are older and are likely to die soon of natural causes.[62][63]

Ant colonies can be long-lived. The queens can live for up to 30 years, and workers live from 1 to 3 years. Males, however, are more transitory, being quite short-lived and surviving for only a few weeks.[64] Ant queens are estimated to live 100 times as long as solitary insects of a similar size.[65]

Ants are active all year long in the tropics, but, in cooler regions, they survive the winter in a state of dormancy known as hibernation. The forms of inactivity are varied and some temperate species have larvae going into the inactive state (diapause), while in others, the adults alone pass the winter in a state of reduced activity.[66]

Reproduction



Alate male ant, *Prenolepis imparis*

A wide range of reproductive strategies have been noted in ant species. Females of many species are known to be capable of reproducing asexually through thelytokous parthenogenesis.[67] Secretions from the male accessory glands in some species can plug the female genital opening and prevent females from re-mating.[68] Most ant species have a system in which only the queen and breeding females have the ability to mate. Contrary to popular belief, some ant nests have multiple queens, while others may exist without queens. Workers with the ability to reproduce are called "gamergates" and colonies that lack queens are then called gamergate colonies; colonies with queens are said to be queen-right.[69]



Ants mating

Drones can also mate with existing queens by entering a foreign colony. When the drone is initially attacked by the workers, it releases a mating pheromone. If recognized as a mate, it will be carried to the queen to mate.[70] Males may also patrol the nest and fight others by grabbing them with their mandibles, piercing their exoskeleton and then marking them with a pheromone. The marked male is interpreted as an invader by worker ants and is killed.[71]



Fertilised meat-eater ant queen beginning to dig a new colony

Most ants are univoltine, producing a new generation each year.[72] During the species-specific breeding period, winged females and winged males, known to entomologists as alates, leave the colony in what is called a nuptial flight. The nuptial flight usually takes place in the late spring or early summer when the weather is hot and humid. Heat makes flying easier and freshly fallen rain makes the ground softer for mated queens to dig nests.[73] Males typically take flight before the females. Males then use visual cues to find a common mating ground, for example, a landmark such as a pine tree to which other males in the area converge. Males secrete a mating pheromone that females follow. Males will mount females in the air, but the actual mating process usually takes place on the ground. Females of some species mate with just one male but in others they may mate with as many as ten or more different males, storing the sperm in their spermathecae.[74]

Mated females then seek a suitable place to begin a colony. There, they break off their wings and begin to lay and care for eggs. The females can selectively fertilise future eggs with the sperm stored to produce diploid workers or lay unfertilized haploid eggs to produce drones. The first workers to hatch are known as nanitics,[75] and are weaker and smaller than later workers, but they begin to serve the colony immediately. They enlarge the nest, forage for food, and care for the other eggs. Species that have multiple queens may have a queen leaving the nest along with some workers to found a colony at a new site,[74] a process akin to swarming in honeybees.

Behaviour and ecology

Communication



Two *Camponotus sericeus* workers communicating through touch and pheromones

Ants communicate with each other using pheromones, sounds, and touch.[76] The use of pheromones as chemical signals is more developed in ants, such as the red harvester ant, than in other hymenopteran groups. Like other insects, ants perceive smells with their long, thin, and mobile antennae. The paired antennae provide information about the direction and intensity of scents. Since most ants live on the ground, they use the soil surface to leave pheromone trails that may be followed by other ants. In species that forage in groups, a forager that finds food marks a trail on the way back to the colony; this trail is followed by other ants, these ants then reinforce the trail when they head back with food to the colony. When the food source is exhausted, no new trails are marked by returning ants and the scent slowly dissipates. This behaviour helps ants deal with changes in their environment. For instance, when an established path to a food source is blocked by an obstacle, the foragers leave the path to explore new routes. If an ant is successful, it leaves a new trail marking the shortest route on its return. Successful trails are followed by more ants, reinforcing better routes and gradually identifying the best path.[77]

Ants use pheromones for more than just making trails. A crushed ant emits an alarm pheromone that sends nearby ants into an attack frenzy and attracts more ants from farther away. Several ant species even use "propaganda pheromones" to confuse enemy ants and make them fight among themselves.[78] Pheromones are produced by a wide range of structures including Dufour's glands, poison glands and glands on the hindgut, pygidium, rectum, sternum, and hind tibia.[65] Pheromones also are exchanged, mixed with food, and passed by trophallaxis, transferring information within the colony.[79] This allows other ants to detect what task group (e.g., foraging or nest maintenance) other colony members belong to.[80] In ant species with queen castes, when the dominant queen stops producing a specific pheromone, workers begin to raise new queens in the colony.[81]

Some ants produce sounds by stridulation, using the gaster segments and their mandibles. Sounds may be used to communicate with colony members or with other species.[82][83]

Defence



A *Plectroctena* sp. attacks another of its kind to protect its territory.

Ants attack and defend themselves by biting and, in many species, by stinging, often injecting or spraying chemicals, such as formic acid in the case of formicine ants, alkaloids and piperidines in fire ants, and a variety of protein components in other ants. Bullet ants (*Paraponera*), located in Central and South America, are considered to have the most painful sting of any insect, although it is usually not fatal to humans. This sting is given the highest rating on the Schmidt Sting Pain Index.

The sting of jack jumper ants can be fatal,[84] and an antivenom has been developed for it.[85]

Fire ants, *Solenopsis* spp., are unique in having a venom sac containing piperidine alkaloids.[86] Their stings are painful and can be dangerous to hypersensitive people.[87]



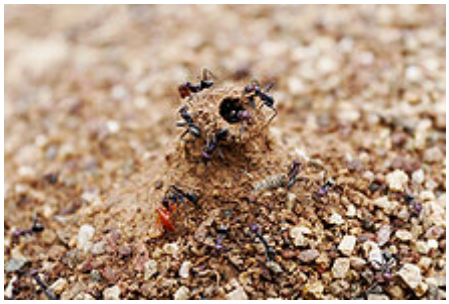
A weaver ant in fighting position, mandibles wide open

Trap-jaw ants of the genus *Odontomachus* are equipped with mandibles called trap-jaws, which snap shut faster than any other predatory appendages within the animal kingdom.[88] One study of *Odontomachus bauri* recorded peak speeds of between 126 and 230 km/h (78 and 143 mph), with the jaws closing within 130 microseconds on average. The ants were also observed to use their jaws as a catapult to eject intruders or fling themselves backward to escape a threat.[88] Before striking, the ant opens its mandibles extremely widely and locks them in this position by an internal mechanism. Energy is stored in a thick band of muscle and explosively released when triggered by the stimulation of sensory organs resembling hairs on the inside of the mandibles. The mandibles also permit slow and fine movements for other tasks. Trap-jaws also are seen in the following genera: *Anochetus*, *Orectognathus*, and *Strumigenys*,[88] plus some members of the Dacetini tribe,[89] which are viewed as examples of convergent evolution.

A Malaysian species of ant in the *Camponotus cylindricus* group has enlarged mandibular glands that extend into their gaster. If combat takes a turn for the worse, a worker may perform a final act of suicidal altruism by rupturing the membrane of its gaster, causing the content of its mandibular glands to burst from the anterior region of its head, spraying a poisonous, corrosive secretion containing acetophenones and other chemicals that immobilise small insect attackers. The worker subsequently dies.[90]

Suicidal defences by workers are also noted in a Brazilian ant, *Forelius pusillus*, where a small group of ants leaves the security of the nest after sealing the entrance from the outside each evening.[91]

In addition to defence against predators, ants need to protect their colonies from pathogens. Some worker ants maintain the hygiene of the colony and their activities include undertaking or *necrophory*, the disposal of dead nest-mates.[92] Oleic acid has been identified as the compound released from dead ants that triggers necrophoric behaviour in *Atta mexicana*[93] while workers of *Linepithema humile* react to the absence of characteristic chemicals (dolichodial and iridomyrmecin) present on the cuticle of their living nestmates to trigger similar behaviour.[94]



Ant mound holes prevent water from entering the nest during rain.

Nests may be protected from physical threats such as flooding and overheating by elaborate nest architecture.[95][96] Workers of *Cataulacus muticus*, an arboreal species that lives in plant hollows, respond to flooding by drinking water inside the nest, and excreting it outside.[97] *Camponotus anderseni*, which nests in the cavities of wood in mangrove habitats, deals with submergence under water by switching to anaerobic respiration.[98]

Learning

Many animals can learn behaviours by imitation, but ants may be the only group apart from mammals where interactive teaching has been observed. A knowledgeable forager of *Temnothorax albipennis* will lead a naive nest-mate to newly discovered food by the process of tandem running. The follower obtains knowledge through its leading tutor. The leader is acutely sensitive to the progress of the follower and slows down when the follower lags and speeds up when the follower gets too close.[99]

Controlled experiments with colonies of *Cerapachys biroi* suggest that an individual may choose nest roles based on her previous experience. An entire generation of identical workers was divided into two groups whose outcome in food foraging was controlled. One group was continually rewarded with prey, while it was made certain that the other failed. As a result, members of the successful group intensified their foraging attempts while the unsuccessful group ventured out fewer and fewer times. A month later, the successful foragers continued in their role while the others had moved to specialise in brood care.[100]

Nest construction

Complex nests are built by many ant species, but other species are nomadic and do not build permanent structures. Ants may form subterranean nests or build them on trees. These nests may be found in the ground, under stones or logs, inside logs, hollow stems, or even acorns. The materials used for construction include soil and plant matter,[74] and ants carefully select their nest sites; *Temnothorax albipennis* will avoid sites with dead ants, as these may indicate the presence of pests or disease. They are quick to abandon established nests at the first sign of threats.[101]



Leaf nest of weaver ants, Pamalican, Philippines

The army ants of South America, such as the *Eciton burchellii* species, and the driver ants of Africa do not build permanent nests, but instead, alternate between nomadism and stages where the workers form a temporary nest (bivouac) from their own bodies, by holding each other together.[102]

Weaver ant (*Oecophylla* spp.) workers build nests in trees by attaching leaves together, first pulling them together with bridges of workers and then inducing their larvae to produce silk as they are moved along the leaf edges. Similar forms of nest construction are seen in some species of *Polyrhachis*.[103]

Formica polyctena, among other ant species, constructs nests that maintain a relatively constant interior temperature that aids in the development of larvae. The ants maintain the nest temperature by choosing the location, nest materials, controlling ventilation and maintaining the heat from solar radiation, worker activity and metabolism, and in some moist nests, microbial activity in the nest materials.[104]

Some ant species, such as those that use natural cavities, can be opportunistic and make use of the controlled micro-climate provided inside human dwellings and other artificial structures to house their colonies and nest structures.[105][106]

Ant bridge



Cultivation of food



Myrmecocystus, honeypot ants, store food to prevent colony famine

Most ants are generalist predators, scavengers, and indirect herbivores,[27] but a few have evolved specialised ways of obtaining nutrition. It is believed that many ant species that engage in indirect herbivory rely on specialized symbiosis with their gut microbes [107] to upgrade the nutritional value of the food they collect [108] and allow them to survive in nitrogen poor regions, such as rainforest canopies.[109] Leafcutter ants (*Atta* and *Acromyrmex*) feed exclusively on a fungus that grows only within their colonies. They continually collect leaves which are taken to the colony, cut into tiny pieces and placed in fungal gardens. Ergates specialise in related tasks according to their sizes. The largest ants cut stalks, smaller workers chew the leaves and the smallest tend the fungus. Leafcutter ants are sensitive enough to recognise the reaction of the fungus to different plant material, apparently detecting chemical signals from the fungus. If a particular type of leaf is found to be toxic to the fungus, the colony will no longer collect it. The ants feed on structures produced by the fungi called *gongylidia*. Symbiotic bacteria on the exterior surface of the ants produce antibiotics that kill bacteria introduced into the nest that may harm the fungi.[110]

Navigation



An ant trail

Foraging ants travel distances of up to 200 metres (700 ft) from their nest [111] and scent trails allow them to find their way back even in the dark. In hot and arid regions, day-foraging ants face death by desiccation, so the ability to find the shortest route back to the nest reduces that risk. Diurnal desert ants of the genus *Cataglyphis* such as the Sahara desert ant navigate by keeping track of direction as well as distance travelled. Distances travelled are measured using an internal pedometer that keeps count of the steps taken[112] and also by evaluating the movement of objects in their visual field (optical flow).[113] Directions are measured using the position of the sun.[114] They integrate this information to find the shortest route back to their nest.[115] Like all ants, they can also make use of visual landmarks when available[116] as well as olfactory and tactile cues to navigate.[117][118] Some species of ant are able to use the Earth's magnetic field for navigation.[119] The compound eyes of ants have specialised cells that detect polarised light from the Sun, which is used to determine direction.[120][121] These polarization detectors are sensitive in the ultraviolet region of the light spectrum.[122] In some army ant species, a group of foragers who become separated from the main column may sometimes turn back on themselves and form a circular ant mill. The workers may then run around continuously until they die of exhaustion.[123]

Locomotion



Play media

Ant in Slow Motion

The female worker ants do not have wings and reproductive females lose their wings after their mating flights in order to begin their colonies. Therefore, unlike their wasp ancestors, most ants travel by walking. Some species are capable of leaping. For example, Jerdon's jumping ant (*Harpegnathos saltator*) is able to jump by synchronising the action of its mid and hind pairs of legs.[124] There are several species of gliding ant including *Cephalotes atratus*; this may be a common trait among arboreal ants with small colonies. Ants with this ability are able to control their horizontal movement so as to catch tree trunks when they fall from atop the forest canopy.[125]

Other species of ants can form chains to bridge gaps over water, underground, or through spaces in vegetation. Some species also form floating rafts that help them survive floods.[126] These rafts may also have a role in allowing ants to colonise islands.[127] *Polyrhachis sokolova*, a species of ant found in Australian mangrove swamps, can swim and live in underwater nests. Since they lack gills, they go to trapped pockets of air in the submerged nests to breathe.[128]

Cooperation and competition

Not all ants have the same kind of societies. The Australian bulldog ants are among the biggest and most basal of ants. Like virtually all ants, they are eusocial, but their social behaviour is poorly developed compared to other species. Each individual hunts alone, using her large eyes instead of chemical senses to find prey.[129]



Meat-eater ants feeding on a cicada: social ants cooperate and collectively gather food

Some species (such as *Tetramorium caespitum*) attack and take over neighbouring ant colonies. Others are less expansionist, but just as aggressive; they invade colonies to steal eggs or larvae, which they either eat or raise as workers or slaves. Extreme specialists among these slave-raiding ants, such as the Amazon ants, are incapable of feeding themselves and need captured workers to survive.[130] Captured workers of enslaved *Temnothorax* species have evolved a counter strategy, destroying just the female pupae of the slave-making *Temnothorax americanus*, but sparing the males (who don't take part in slave-raiding as adults).[131]



A worker *Harpegnathos saltator* (a jumping ant) engaged in battle with a rival colony's queen

Ants identify kin and nestmates through their scent, which comes from hydrocarbon-laced secretions that coat their exoskeletons. If an ant is separated from its original colony, it will eventually lose the colony scent. Any ant that enters a colony without a matching scent will be attacked.[132] Also, the reason why two separate colonies of ants will attack each other even if they are of the same species is because the genes responsible for pheromone production are different between them. The Argentine ant, however, does not have this characteristic, due to lack of genetic diversity, and has become a global pest because of it.

Parasitic ant species enter the colonies of host ants and establish themselves as social parasites; species such as *Strumigenys xenos* are entirely parasitic and do not have workers, but instead, rely on the food gathered by their *Strumigenys perplexa* hosts.[133][134] This form of parasitism is seen across many ant genera, but the parasitic ant is usually a species that is closely related to its host. A variety of methods are employed to enter the nest of the host ant. A parasitic queen may enter the host nest before the first brood has hatched, establishing herself prior to development of a colony scent. Other species use pheromones to confuse the host ants or to trick them into carrying the parasitic queen into the nest. Some simply fight their way into the nest.[135]

A conflict between the sexes of a species is seen in some species of ants with these reproducers apparently competing to produce offspring that are as closely related to them as possible. The most extreme form involves the production of clonal offspring. An extreme of sexual conflict is seen in *Wasmannia auropunctata*, where the queens produce diploid daughters by thelytokous parthenogenesis and males produce clones by a process whereby a diploid egg loses its maternal contribution to produce haploid males who are clones of the father.[136]

Relationships with other organisms

Ants form symbiotic associations with a range of species, including other ant species, other insects, plants, and fungi. They also are preyed on by many animals and even certain fungi. Some arthropod species spend part of their lives within ant nests, either preying on ants, their larvae, and eggs, consuming the food stores of the ants, or avoiding predators. These inquilines may bear a close resemblance to ants. The nature of this ant mimicry (myrmecomorphy) varies, with some cases involving Batesian mimicry, where the mimic reduces the risk of predation. Others show Wasmannian mimicry, a form of mimicry seen only in inquilines.[137][138]



The spider *Myrmarachne plataleoides* (female shown) mimics weaver ants to avoid predators.



An ant collects honeydew from an aphid

Aphids and other hemipteran insects secrete a sweet liquid called honeydew, when they feed on plant sap. The sugars in honeydew are a high-energy food source, which many ant species collect.[139] In some cases, the aphids secrete the honeydew in response to ants tapping them with their antennae. The ants in turn keep predators away from the aphids and will move them from one feeding location to another. When migrating to a new area, many colonies will take the aphids with them, to ensure a continued supply of honeydew. Ants also tend mealybugs to harvest their honeydew. Mealybugs may become a serious pest of pineapples if ants are present to protect mealybugs from their natural enemies.[140]

Myrmecophilous (ant-loving) caterpillars of the butterfly family Lycaenidae (e.g., blues, coppers, or hairstreaks) are herded by the ants, led to feeding areas in the daytime, and brought inside the ants' nest at night. The caterpillars have a gland which secretes honeydew when the ants massage them. Some caterpillars produce vibrations and sounds that are perceived by the ants.[141] A similar adaptation can be seen in Grizzled skipper butterflies that emit vibrations by expanding their wings in order to communicate with ants, which are natural predators of these butterflies.[142] Other caterpillars have evolved from ant-loving to ant-eating: these myrmecophagous caterpillars secrete a pheromone that makes the ants act as if the caterpillar is one of their own larvae. The caterpillar is then taken into the ant nest where it feeds on the ant larvae.[143] A number of specialized bacterial have been found as endosymbionts in ant guts. Some of the dominant bacteria belong to the order Rhizobiales whose members are known for being nitrogen-fixing symbionts in legumes but the species found in ant lack the ability to fix nitrogen.[144][145] Fungus-growing ants that make up the tribe Attini, including leafcutter ants, cultivate certain species of fungus in the genera *Leucoagaricus* or *Leucocoprinus* of the family Agaricaceae. In this ant-fungus mutualism, both species depend on each other for survival. The ant *Allomerus decemarticulatus* has evolved a three-way association with the host plant, *Hirtella physophora* (Chrysobalanaceae), and a sticky fungus which is used to trap their insect prey.[146]

Lemon ants make devil's gardens by killing surrounding plants with their stings and leaving a pure patch of lemon ant trees, (*Duroia hirsuta*). This modification of the forest provides the ants with more nesting sites inside the stems of the *Duroia* trees.[147] Although some ants obtain nectar from flowers, pollination by ants is somewhat rare, one example being of the pollination of the orchid *Leporella fimbriata* which induces male *Myrmecia urens* to pseudocopulate with the flowers, transferring pollen in the process.[148] One theory that has been proposed for the rarity of pollination is that the secretions of the metapleural gland inactivate and reduce the viability of pollen.[149][150] Some plants have special nectar exuding structures, extrafloral nectaries, that provide food for ants, which in turn protect the plant from more damaging herbivorous insects.[151] Species such as the bullhorn acacia (*Acacia cornigera*) in Central America have



Ants may obtain nectar from flowers such as the dandelion but are only rarely known to pollinate flowers.

hollow thorns that house colonies of stinging ants (*Pseudomyrmex ferruginea*) who defend the tree against insects, browsing mammals, and epiphytic vines. Isotopic labelling studies suggest that plants also obtain nitrogen from the ants.[152] In return, the ants obtain food from protein- and lipid-rich Beltian bodies. In Fiji *Philidris nagasau* (Dolichoderinae) are known to selectively grow species of epiphytic *Squamellaria* (Rubiaceae) which produce large domatia inside which the ant colonies nest. The ants plant the seeds and the domatia of young seedling are immediately occupied and the ant faeces in them contribute to rapid growth.[153] Similar dispersal associations are found with other dolichoderines in the region as well.[154] Another example of this type of ectosymbiosis comes from the *Macaranga* tree, which has stems adapted to house colonies of *Crematogaster* ants.[155]

Many plant species have seeds that are adapted for dispersal by ants.[156] Seed dispersal by ants or myrmecochory is widespread, and new estimates suggest that nearly 9% of all plant species may have such ant associations.[157][156] Often, seed-dispersing ants perform directed dispersal, depositing the seeds in locations that increase the likelihood of seed survival to reproduction.[158] Some plants in arid, fire-prone systems are particularly dependent on ants for their survival and dispersal as the seeds are transported to safety below the ground.[159] Many ant-dispersed seeds have special external structures, elaiosomes, that are sought after by ants as food.[160]

A convergence, possibly a form of mimicry, is seen in the eggs of stick insects. They have an edible elaiosome-like structure and are taken into the ant nest where the young hatch.[161]



A meat ant tending a common leafhopper nymph

Most ants are predatory and some prey on and obtain food from other social insects including other ants. Some species specialise in preying on termites (*Megaponera* and *Termitopone*) while a few Cerapachyinae prey on other ants.[111] Some termites, including *Nasutitermes corniger*, form associations with certain ant species to keep away predatory ant species.[162] The tropical wasp *Mischocyttarus drewseni* coats the pedicel of its nest with an ant-repellent chemical.[163] It is suggested that many tropical wasps may build their nests in trees and cover them to protect themselves from ants. Other wasps, such as *A. multipicta*, defend against ants by blasting them off the nest with bursts of wing buzzing.[164] Stingless bees (*Trigona* and *Melipona*) use chemical defences against ants.[111]

Flies in the Old World genus *Bengalia* (Calliphoridae) prey on ants and are kleptoparasites, snatching prey or brood from the mandibles of adult ants.[165] Wingless and legless females of the Malaysian phorid fly (*Vestigipoda myrmolarvoidea*) live in the nests of ants of the genus *Aenictus* and are cared for by the ants.[165]

Fungi in the genera *Cordyceps* and *Ophiocordyceps* infect ants. Ants react to their infection by climbing up plants and sinking their mandibles into plant tissue. The fungus kills the ants, grows on their remains, and produces a fruiting body. It appears that the fungus alters the behaviour of the ant to help disperse its spores [166] in a microhabitat that best suits the fungus.[167] Strepsipteran parasites also manipulate their ant host to climb grass stems, to help the parasite find mates.[168]

A nematode (*Myrmeconema neotropicum*) that infects canopy ants (*Cephalotes atratus*) causes the black-coloured gasters of workers to turn red. The parasite also alters the behaviour of the ant, causing them to carry their gasters high. The conspicuous red gasters are mistaken by birds for ripe fruits, such as *Hyeronima alchorneoides*, and eaten. The droppings of the bird are collected by other ants and fed to their young, leading to further spread of the nematode.[169]

South American poison dart frogs in the genus *Dendrobates* feed mainly on ants, and the toxins in their skin may come from the ants.[170]

Army ants forage in a wide roving column, attacking any animals in that path that are unable to escape. In Central and South America, *Eciton burchellii* is the swarming ant most commonly attended by "ant-following" birds such as antbirds and woodcreepers.[171][172] This behaviour was once considered mutualistic, but later studies found the birds to be parasitic. Direct

kleptoparasitism (birds stealing food from the ants' grasp) is rare and has been noted in Inca doves which pick seeds at nest entrances as they are being transported by species of *Pogonomyrmex*.[173] Birds that follow ants eat many prey insects and thus decrease the foraging success of ants.[174] Birds indulge in a peculiar behaviour called anting that, as yet, is not fully understood. Here birds rest on ant nests, or pick and drop ants onto their wings and feathers; this may be a means to remove ectoparasites from the birds.


Spiders sometimes feed on ants.

Anteaters, aardvarks, pangolins, echidnas and numbats have special adaptations for living on a diet of ants. These adaptations include long, sticky tongues to capture ants and strong claws to break into ant nests. Brown bears (*Ursus arctos*) have been found to feed on ants. About 12%, 16%, and 4% of their faecal volume in spring, summer, and autumn, respectively, is composed of ants.[175]

Relationship with humans

Ants perform many ecological roles that are beneficial to humans, including the suppression of pest populations and aeration of the soil. The use of weaver ants in citrus cultivation in southern China is considered one of the oldest known applications of biological control.[14] On the other hand, ants may become nuisances when they invade buildings, or cause economic losses.


Weaver ants are used as a biological control for citrus cultivation in southern China.

In some parts of the world (mainly Africa and South America), large ants, especially army ants, are used as surgical sutures. The wound is pressed together and ants are applied along it. The ant seizes the edges of the wound in its mandibles and locks in place. The body is then cut off and the head and mandibles remain in place to close the wound.[176][177][178] The large heads of the dinergates (soldiers) of the leafcutting ant *Atta cephalotes* are also used by native surgeons in closing wounds.[179]

Some ants have toxic venom and are of medical importance. The species include *Paraponera clavata* (tocandira) and *Dinoponera* spp. (false tocandiras) of South America [180] and the *Myrmecia* ants of Australia.[181]

In South Africa, ants are used to help harvest the seeds of rooibos (*Aspalathus linearis*), a plant used to make a herbal tea. The plant disperses its seeds widely, making manual collection difficult. Black ants collect and store these and other seeds in their nest, where humans can gather them *en masse*. Up to half a pound (200 g) of seeds may be collected from one ant-heap.[182][183]

Although most ants survive attempts by humans to eradicate them, a few are highly endangered. These tend to be island species that have evolved specialized traits and risk being displaced by introduced ant species. Examples include the critically endangered Sri Lankan relict ant (*Aneuretus simoni*) and *Adetomyrma venatrix* of Madagascar.[184]

It has been estimated by E.O. Wilson that the total number of individual ants alive in the world at any one time is between one and ten quadrillion (short scale) (i.e., between 10^{15} and 10^{16}). According to this estimate, the total biomass of all the ants in the world is approximately equal to the total biomass of the entire human race.[185] Also, according to this estimate, there are approximately 1 million ants for every human on Earth.[186]

As food



Roasted ants in Colombia



Ant larvae for sale in Isaan, Thailand

Ants and their larvae are eaten in different parts of the world. The eggs of two species of ants are used in Mexican *escamoles*. They are considered a form of insect caviar and can sell for as much as US$40 per pound ($90/kg) because they are seasonal and hard to find. In the Colombian department of Santander, *hormigas culonas* (roughly interpreted as "large-bottomed ants") *Atta laevigata* are toasted alive and eaten.[187]

In areas of India, and throughout Burma and Thailand, a paste of the green weaver ant (*Oecophylla smaragdina*) is served as a condiment with curry.[188] Weaver ant eggs and larvae, as well as the ants, may be used in a Thai salad, *yam* (Thai: ยำ), in a dish called *yam khai mot daeng* (Thai: ยำไข่มดแดง) or red ant egg salad, a dish that comes from the Issan or north-eastern region of Thailand. Saville-Kent, in the *Naturalist in Australia* wrote "Beauty, in the case of the green ant, is more than skin-deep. Their attractive, almost sweetmeat-like translucency possibly invited the first essays at their consumption by the human species". Mashed up in water, after the manner of lemon squash, "these ants form a pleasant acid drink which is held in high favor by the natives of North Queensland, and is even appreciated by many European palates".[189]

In his *First Summer in the Sierra*, John Muir notes that the Digger Indians of California ate the tickling, acid gasters of the large jet-black carpenter ants. The Mexican Indians eat the replete workers, or living honey-pots, of the honey ant (*Myrmecocystus*).[189]

As pests

Some ant species are considered as pests, primarily those that occur in human habitations, where their presence is often problematic. For example, the presence of ants would be undesirable in sterile places such as hospitals or kitchens. Some species or genera commonly categorized as pests include the Argentine ant, pavement ant, yellow crazy ant, banded sugar ant, pharaoh ant, carpenter ants, odorous house ant, red imported fire ant, and European fire ant. Some ants will raid stored food, others may damage indoor structures, some can damage agricultural crops directly (or by aiding sucking pests), and some will sting or bite.[15] The adaptive nature of ant colonies make it nearly impossible to eliminate entire colonies and most pest management practices aim to control local populations and tend to be temporary solutions. Ant populations are managed by a combination of approaches that make use of chemical, biological and physical methods. Chemical methods include the use of insecticidal bait which is gathered by ants as food and brought back to the nest where the poison is inadvertently spread to other colony members through trophallaxis. Management is based on the species and techniques can vary according to the location and circumstance.[15]



The tiny pharaoh ant is a major pest in hospitals and office blocks; it can make nests between sheets of paper.

In science and technology

Observed by humans since the dawn of history, the behaviour of ants has been documented and the subject of early writings and fables passed from one century to another. Those using scientific methods, myrmecologists, study ants in the laboratory and in their natural conditions. Their complex and variable social structures have made ants ideal model organisms. Ultraviolet vision

was first discovered in ants by Sir John Lubbock in 1881.[190] Studies on ants have tested hypotheses in ecology and sociobiology, and have been particularly important in examining the predictions of theories of kin selection and evolutionarily stable strategies.[191] Ant colonies may be studied by rearing or temporarily maintaining them in *formicaria*, specially constructed glass framed enclosures.[192] Individuals may be tracked for study by marking them with dots of colours.[193]



Camponotus nearcticus workers travelling between two formicaria through connector tubing

The successful techniques used by ant colonies have been studied in computer science and robotics to produce distributed and fault-tolerant systems for solving problems, for example Ant colony optimization and Ant robotics. This area of biomimetics has led to studies of ant locomotion, search engines that make use of "foraging trails", fault-tolerant storage, and networking algorithms.[13]

As pets

From the late 1950s through the late 1970s, ant farms were popular educational children's toys in the United States. Some later commercial versions use transparent gel instead of soil, allowing greater visibility at the cost of stressing the ants with unnatural light.[194]

In culture



Aesop's ants: picture by Milo Winter, 1888–1956

Anthropomorphised ants have often been used in fables and children's stories to represent industriousness and cooperative effort. They also are mentioned in religious texts.[195][196] In the Book of Proverbs in the Bible, ants are held up as a good example for humans for their hard work and cooperation.[197] Aesop did the same in his fable The Ant and the Grasshopper. In the Quran, Sulayman is said to have heard and understood an ant warning other ants to return home to avoid being accidentally crushed by Sulayman and his marching army. [Quran 27:18 (http://www.perseus.tufts.edu/hopper/text?doc=Perseus%3Atext%3A2002.02.0006%3Asura%3D27%3Averse%3D18)][198] In parts of Africa, ants are considered to be the messengers of the deities. Some Native American mythology, such as the Hopi mythology, considers ants as the very first animals. Ant bites are often said to have curative properties. The sting of some species of *Pseudomyrmex* is claimed to give fever relief.[199] Ant bites are used in the initiation ceremonies of some Amazon Indian cultures as a test of endurance.[200][201]

Ant society has always fascinated humans and has been written about both humorously and seriously. Mark Twain wrote about ants in his 1880 book *A Tramp Abroad*.[202] Some modern authors have used the example of the ants to comment on the relationship between society and the individual. Examples are Robert Frost in his poem "Departmental" and T. H. White in his fantasy novel *The Once and Future King*. The plot in French entomologist and writer Bernard Werber's *Les Fourmis* science-fiction trilogy is divided between the worlds of ants and humans; ants and their behaviour is described using contemporary scientific knowledge. H.G. Wells wrote about intelligent ants destroying human settlements in Brazil and threatening human civilization in his 1905 science-fiction short story, *The Empire of the Ants.* In more recent times, animated cartoons and 3-D animated films featuring ants have been produced including *Antz*, *A Bug's Life*, *The Ant Bully*, *The Ant and the Aardvark*, *Ferdy the Ant* and *Atom Ant.* Renowned myrmecologist E. O. Wilson wrote a short story, "Trailhead" in 2010 for *The New Yorker*

magazine, which describes the life and death of an ant-queen and the rise and fall of her colony, from an ants' point of view.[203] The French neuroanatomist, psychiatrist and eugenicist Auguste Forel believed that ant societies were models for human society. He published a five volume work from 1921 to 1923 that examined ant biology and society.[204]

In the early 1990s, the video game *SimAnt*, which simulated an ant colony, won the 1992 Codie award for "Best Simulation Program".[205]

Ants also are quite popular inspiration for many science-fiction insectoids, such as the Formics of *Ender's Game*, the Bugs of *Starship Troopers*, the giant ants in the films *Them!* and *Empire of the Ants*, Marvel Comics' super hero Ant-Man, and ants mutated into super-intelligence in *Phase IV*. In computer strategy games, ant-based species often benefit from increased production rates due to their single-minded focus, such as the Klackons in the *Master of Orion* series of games or the ChCht in *Deadlock II*. These characters are often credited with a hive mind, a common misconception about ant colonies.[206]

See also

- Ant robotics
- Ant venom
- Glossary of ant terms
- International Union for the Study of Social Insects
- *Myrmecological News* (journal)
- Task allocation and partitioning of social insects

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External links

- AntWeb from The California Academy of Sciences (http://www.antweb.org/)
- AntBase – a taxonomic database with literature sources (http://antbase.org/)
- AntWiki – Bringing Ants to the World (http://www.antwiki.org/wiki/Welcome_to_AntWiki)
- Ant Species Fact Sheets (http://www.pestworld.org/pest-guide/ants/) from the National Pest Management Association on Argentine, Carpenter, Pharaoh, Odorous, and other ant species

- Ant Genera of the World – distribution maps (http://www.antwiki.org/wiki/Category:Genus_Distribution_Map)
- The super-nettles. A dermatologist's guide to ants-in-the-plants (http://www.botanical-dermatology-database.info/BotDermReviews/Myrmecophytes.html)

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Argentine ant

The **Argentine ant** (*Linepithema humile*), formerly *Iridomyrmex humilis*, is an ant native to northern Argentina, Uruguay, Paraguay, Bolivia and southern Brazil. It is an invasive species that has been established in many Mediterranean climate areas,[1] inadvertently introduced by humans to many places, including South Africa, New Zealand, Japan, Easter Island, Australia, Europe, Hawaii, and continental United States.[2][3]

Argentine ant



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	Dolichoderinae
Genus:	*Linepithema*
Species:	***L. humile***

Binomial name

Linepithema humile
(Mayr, 1868)

Contents

Description

Distribution
Global "mega-colony"

Behavior

Reproduction and seasonal colony trends

Impact

Pest control

See also

References

External links

Description

The worker ants are 1.6–2.8 millimetres (0.06–0.11 in) long[4][5] and can easily squeeze through cracks and holes as small as 1 millimetre (0.04 in) in size. Queens are 4.2–6.4 millimetres (0.17–0.25 in) long,[4] much smaller than other species of ants. These ants will set up quarters in the ground, in cracks in concrete walls, in spaces between boards and timbers, even among belongings in human dwellings. In natural areas, they generally nest shallowly in loose leaf litter or beneath small stones, due to their poor ability to dig deeper nests. However, if a deeper nesting ant species abandons their nest, Argentine ant colonies will readily take over the space.

Austrian entomologist Gustav L. Mayr identified the first specimens of *Hypoclinea humilis* in the vicinity of Buenos Aires, Argentina in 1866. This species was shortly transferred to the genus *Iridomyrmex*, and finally to *Linepithema* in the early 1990s.

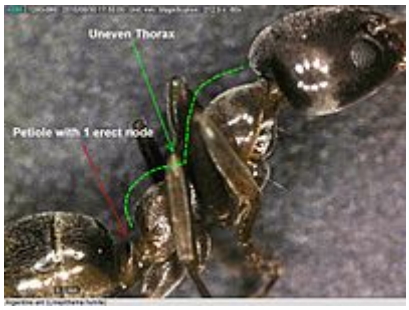
Distribution

The native range of Argentine ants is limited to around major waterways in the lowland areas of the Paraná River drainage. They have recently spread into parts of Argentina, Brazil, Chile, Colombia, Ecuador, and Peru.[6] The species has become established in at least 15 countries throughout the world, on six continents, as well as many oceanic islands.[7]

Global "mega-colony"



Typical size of worker ants found in Southern California.



These markers can help identify Argentine ants.

According to research published in *Insectes Sociaux* in 2009, it was discovered that ants from three Argentine ant supercolonies in America, Europe, and Japan, that were previously thought to be separate, were in fact most likely to be genetically related. The three colonies in question were one in Europe, stretching 6,000 km (3,700 mi) along the Mediterranean coast, the "Californian large" colony, stretching 900 km (560 mi) along the coast of California, and a third on the west coast of Japan.[8][9]

Based on a similarity in the chemical profile of hydrocarbons on the cuticles of the ants from each colony, and on the ants' non-aggressive and grooming behaviour when interacting, compared to their behaviour when mixing with ants from other super-colonies from the coast of Catalonia in Spain and from Kobe in Japan, researchers concluded that the three colonies studied actually represented a single global super-colony.[8][9]

The researchers stated that "enormous extent of this population is paralleled only by human society", and had probably been spread and maintained by human travel.[8][9]

Behavior



Argentine ants on a dead horse-fly

They have been extraordinarily successful, in part, because different nests of the introduced Argentine ants seldom attack or compete with each other, unlike most other species of ant. In their introduced range, their genetic makeup is so uniform that individuals from one nest can mingle in a neighboring nest without being attacked. Thus, in most of their introduced range, they form supercolonies. "Some ants have an extraordinary social organization, called unicoloniality, whereby individuals mix freely among physically separated nests. This type of social organization is not only a key attribute responsible for the ecological domination of these ants, but also an evolutionary paradox and a potential problem for kin selection theory because relatedness between nest mates is effectively zero."[10] The Very Large Colony, which covers territory from San Diego to beyond San Francisco, may have a population of nearly one trillion individuals.[11]

Conflict does occur between members of different supercolonies. In 1997, UC San Diego researchers observed fighting between different Argentine ants kept in lab, and in 2004 scientists began to map out the boundaries of the different supercolonies that clashed in San Diego. On the border of the Very Large Colony and the Lake Hodges Colony thirty million ants die each year on a battlefront that covers miles.[12]

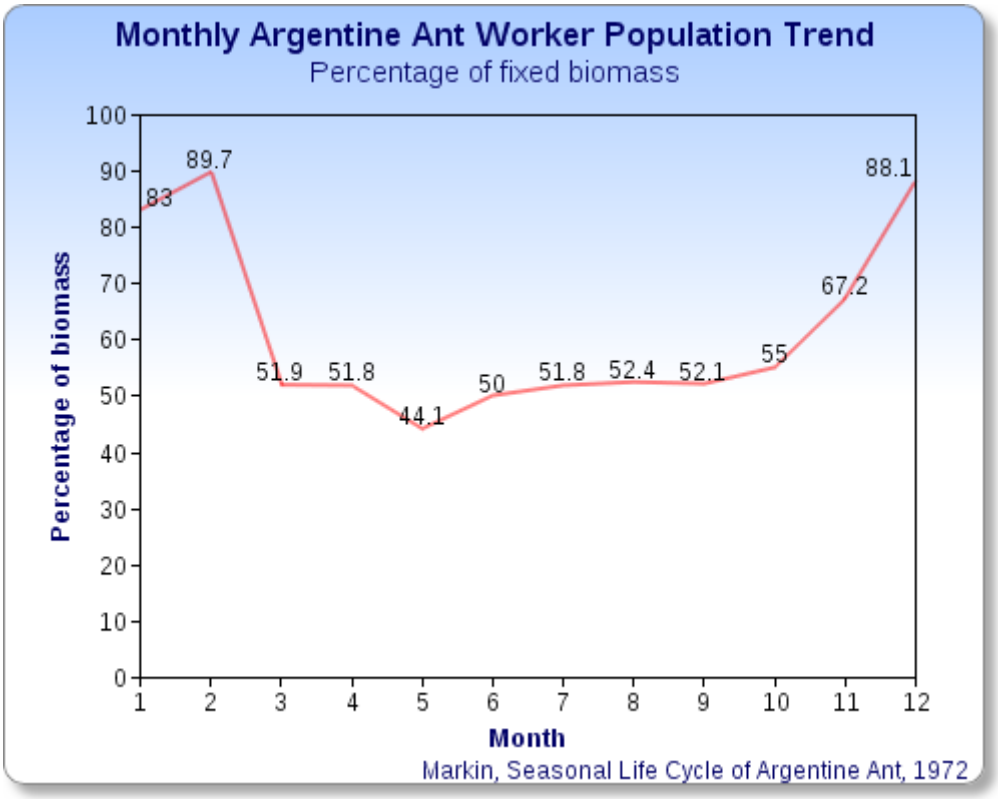
In contrast, native populations are more genetically diverse, genetically differentiated (among colonies and across space), and form colonies that are much smaller than the supercolonies that dominate the introduced range. Argentine ants in their native South America also co-exist with many other species of ants, and do not attain the high population densities that characterize introduced populations.[13]

In a series of experiments, ants of the same colony were isolated and fed different diets. The hydrocarbons from the diet were eventually incorporated into the cuticle of the subjects. Those that had the same diet appeared to recognize one another as kin. Those who had at least some overlap in dietary composition also appeared to react non-aggressively to one another. These

interactions contrasts drastically with the groups that fed on completely different sources, such as those who lived off flies and those that fed on grasshoppers. The groups appeared to have incorporated hydrocarbons that were not similar to the others and created an unfamiliar identity cue. These groups reacted violently towards each other. This suggests that dietary factors affect the recognition cues for colony members.[14][15]

Reproduction and seasonal colony trends

Like workers in many other ant species, Argentine ant workers are unable to lay reproductive eggs but can direct the development of eggs into reproductive females; the production of males appears to be controlled by the amount of food available to the larvae.[16] Argentine ant colonies almost invariably have many reproductive queens, as many as eight for every 1,000 workers. The queens seldom or never disperse in winged form. Instead, colonies reproduce by budding off into new units. As few as ten workers and a single queen can establish a new colony.



The seasonal low occurs in mid-winter, when 90% of a representative colony consisted of workers and the remainder of queens, and no reproductive activity and minimal birthing. Eggs are produced in late-winter, nearly all of which hatch into sexual forms by May. Mating occurs after the females emerge. Worker production increases steadily from mid-March to October, after which their numbers are not replenished; thus, their numbers drop steadily over the winter months.[17]

Colonies in the Argentine ant's native habitat are kept within a range of ten to one hundred meters by colonies of interspecific and intraspecific rivals. As the colonies expand, they appear to form fluctuating territory borders, which contract and expand on a seasonal and conditional basis. There is an expansive push outward in the summer months, with a retreating motion in the winter. This has to do with soil moisture and temperature conditions.[18] At the edges of these borders are either rival *L. humile* colonies or other obstacles that prevent further expansion, such as an inhospitable environment for nesting.[18]

Impact

The ants are ranked among the world's 100 worst animal invaders.[19] In its introduced range, the Argentine ant often displaces most or all native ants. This can, in turn, imperil other species in the ecosystem, such as native plants that depend on native ants for seed dispersal, or lizards that depend on native ants for food. For example, the recent severe decline in coastal horned lizards in southern California is closely tied to Argentine ants displacing native ant species on which the lizards feed.[20]

Argentine ants sometimes tend aphid, mealybug, and scale insect colonies,[21] sometimes relocating the parasites to unaffected plants, and their protection of these plant pests from predators and parasitoids can cause problems in agricultural areas.[22] In return for this protection, the ants benefit by feeding off an excretion known as honeydew. Thus, when Argentine ants invade an

agricultural area, the population densities of these plant parasites increase and so does the damage they cause to crops. There is also evidence that the presence of Argentine ant may decrease the number of pollinators that visit natural flowering plants via predation on the larvae of the pollinators.[23]

Pest control

Argentine ants are a common household pest, often entering structures in search of food or water (particularly during dry or hot weather), or to escape flooded nests during periods of heavy rainfall. When they invade a kitchen, it is not uncommon to see two or three queens foraging along with the workers. Due to the large number of queens, eliminating a single queen does not stop the colony's ability to breed.



Argentine ants accessing a commercial bait station commonly available in the United States

A non-toxic way to eradicate these ants is by dusting the trails, feeding sites and nest entrances with diatomaceous earth, if the problem is inside the home use food grade earth.

Borate-sucrose water baits are toxic to Argentine ants, when the bait is 25% water, with 0.5–1.0% boric acid or borate salts. [24] [25]

Due to their nesting behavior and presence of numerous queens in each colony, it is generally impractical to spray Argentine ants with pesticides or to use boiling water as with mound building ants. Spraying with pesticides has occasionally stimulated increased egg-laying by the queens, compounding the problem. Pest control usually requires exploiting their omnivorous dietary habits, through use of slow-acting poison bait (e.g. fipronil, hydramethylnon, sulfluramid), which will be carried back to the nest by the workers, eventually killing all the individuals, including the queens. It may take four to five days to eradicate a colony in this manner.

Researchers from the University of California, Irvine, have developed a way to use the scent of Argentine ants against them.[26] The exoskeletons of the ants are covered with a hydrocarbon-laced secretion. They made a compound that is different, but similar, to the one that coats the ants. If the chemical is applied to an ant, the other members of the colony will kill it.[27] The chemical method may be effective in combination with other methods.

Another approach for a large scale control of the Argentine ant has been proposed by researchers from Japan, who showed that it is possible to disrupt its trails with synthetic pheromones.[28] This has been confirmed in various later trials by a New Zealand-led team in Hawaii [29] and by researchers from Victoria University of Wellington who showed that this approach is beneficial for other local ant species.[30]

See also

- Linepithema humile virus 1, a virus carried by Argentine ants

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External links

- National Pest Management Association. "Argentine Ant Fact Sheet" (http://www.pestworld.org/pest-guide/ants/argentine-ants/). with information on habits, habitat and prevention
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Carpenter ant

Carpenter ants (*Camponotus* spp.) are large (0.3 to 1.0 in or 0.76 to 2.54 cm) ants indigenous to many forested parts of the world.[2]

They build nests inside wood consisting of galleries chewed out with their mandibles, preferably in dead, damp wood. However, unlike termites, they do not consume wood.[3] Sometimes, carpenter ants hollow out sections of trees. They also commonly infest wooden buildings and structures, and are a widespread nuisance and major cause of structural damage. Nevertheless, their ability to excavate wood helps in forest decomposition. One of the most familiar species associated with human habitation in the United States is the black carpenter ant (*Camponotus pennsylvanicus*). The genus includes over 1,000 species.[4] They also farm aphids. In the farming, the ants protect the aphids while they excrete a sugary fluid called honeydew, which the ants get by stroking the aphids with their antennae.

Contents

Habitat
- Food
- Symbionts

Behavior and ecology
- Nesting
- Relatedness
- Kin recognition
- Kin altruism
- Pheromones
- Social immunity
- Polygyny

Exploding ants

Selected species

Relationship with humans
- As pests
- As food

References
- Cited texts

Further reading

External links

Habitat

Carpenter ant

Temporal range: Eocene – Recent

52.2–0 Ma

Pre Є Є O S D C P T J K PgN



Camponotus sp. (worker)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	Formicinae
Tribe:	Camponotini
Genus:	*Camponotus* Mayr, 1861

Type species

Formica ligniperda Latreille, 1802

Diversity

> 1,000 species

Synonyms[1]

- *Condylomyrma* Santschi, 1928
- *Dolophra* Wu, J. & Wang, 1994
- *Myrmocamelus* Forel, 1914
- *Myrmolophus* Emery, 1920

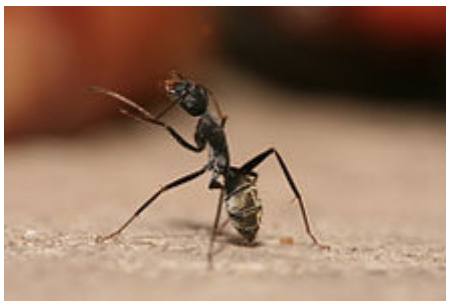
Carpenter ant species reside both outdoors and indoors in moist, decaying, or hollow wood, most commonly in forest environments. They cut "galleries" into the wood grain to provide passageways to allow for movement between different sections of the nest. Certain parts of a house, such as around and under windows, roof eaves, decks and porches, are more likely to be infested by carpenter ants because these areas are most vulnerable to moisture.

Carpenter ants have been known to construct extensive underground tunneling systems. These systems often lead to an end at some food source – often aphid colonies, where the ants extract and feed on honeydew. These tunneling systems also often exist in trees. The colonies typically include a central "parent" colony surrounded and supplemented by smaller satellite colonies.[5]

- *Myrmosaga* Forel, 1912
- *Myrmoturba* Forel, 1912
- *Neocolobopsis* Borgmeier, 1928
- *Neomyrmamblys* Wheeler, W.M., 1921
- *Orthonotus* Ashmead, 1905
- *Paleosminthurus* Pierce & Gibron, 1962
- *Paracolobopsis* Emery, 1920
- *Shanwangella* Zhang, J., 1989

Food

Carpenter ants are considered both predators and scavengers. These ants are foragers that typically eat parts of other dead insects or substances derived from other insects. Common foods for them include insect parts, "honeydew" produced by aphids, or extrafloral nectar from plants. They are also known for eating other sugary liquids such as honey, syrup, or juices. Carpenter ants can increase the survivability of aphids when they tend them. They tend many aphid species but can also express preference for specific ones.



Carpenter ant cleaning antennae

Most species of carpenter ants forage at night. When foraging, they usually collect and consume dead insects. Some species less commonly collect live insects. When they discover a dead insect, workers surround it and extract its bodily fluids to be carried back to the nest. The remaining chitin-based shell is left behind. Occasionally, the ants bring the chitinous head of the insect back to the nest, where they also extract its inner tissue.[6] The ants can forage individually or in small or large groups, though they often opt to do so individually. Different colonies in close proximity may have overlapping foraging regions, though they typically do not assist each other in foraging. Their main food sources normally include proteins and carbohydrates.[7] Instances of carpenter ants bleeding Chinese elm trees for the sap have been observed in the northern Arizona region. These instances may be rare as the colonies vastly exceeded the standard size of carpenter ant colonies elsewhere.[8] When workers find food sources, they communicate this information to the rest of the nest. They use biochemical pheromones to mark the shortest path that can be taken from the nest to the source. When a sizable number of workers follows this trail, the strength of the cue increases and a foraging trail is established. This ends when the food source is depleted. The workers will then feed the queen and the larvae by consuming the food they have found, and regurgitating the food at the nest. Foraging trails can either be under or above ground.[9]



Carpenter ants carrying a dead bee



A major worker of *Camponotus* sp.

Although carpenter ants do not tend to be extremely aggressive, they have developed mechanisms to maximize their provision from a food source when that same food source is visited by a competing organism. This is accomplished in different ways. Sometimes they colonize an area near a relatively static food

supply. More often, they develop a systemic way to visit the food source with alternating trips by different individual ants or groups. This allows them to decrease the gains of intruders because the intruders tend to visit in a scattered, random, and unorganized manner. The ants, however, visit the sources systematically such that they lower the mean standing crop. They tend to visit more resource-dense food areas in an attempt to minimize resource availability for others. That is, the more systematic the foraging behavior of the ants, the more random that of its competitors.[10]

Contrary to popular belief, carpenter ants do not actually eat wood because they are unable to digest cellulose. They only create tunnels and nests within it.[11]

Symbionts

All ants in this genus, and some related genera, possess an obligate bacterial endosymbiont called *Blochmannia*.[12] This bacterium has a small genome, and retains genes to biosynthesize essential amino acids and other nutrients. This suggests the bacterium plays a role in ant nutrition. Many *Camponotus* species are also infected with *Wolbachia*, another endosymbiont that is widespread across insect groups.

Behavior and ecology

Nesting

Carpenter ants work to build the nests that house eggs in environments with usually high humidity due to their sensitivity to environmental humidity. These nests are called primary nests. Satellite nests are constructed once the primary nest is established and has begun to mature. Residents of satellite nests include older larvae, pupae, and some winged individuals. Only eggs, the newly hatched larvae, workers, and the queen reside in the primary nests. As satellite nests do not have environmentally sensitive eggs, the ants can construct them in rather diverse locations that can actually be relatively dry.[13] Some species, like *Camponotus vagus*, builds the nest in a dry place, usually in wood.



Play media

Carpenter ant colony in an old fir stump

Nuptial flight

When conditions are warm and humid, winged males and females participate in a nuptial flight. They emerge from their satellite nests and females mate with a number of males while in flight. The males die after mating. These newly fertilized queens discard their wings and search for new areas to establish primary nests. The queens build new nests and deposit around 20 eggs, nurturing them as they grow until worker ants emerge. The worker ants eventually assist her in caring for the brood as she lays more eggs. After a few years, reproductive winged ants are born, allowing for the making of new colonies. Again, satellite nests will be established and the process will repeat itself.[13]



Carpenter ants in a tree

Relatedness

Relatedness is the probability that a gene in one individual is an identical copy, by descent, of a gene in another individual. It is essentially a measure of how closely related two individuals are with respect to a gene. It is quantified by the coefficient of relatedness, which is a number between zero and one. The larger the value, the more two individuals are "related". Carpenter ants are social hymenopteran insects. This means the relatedness between offspring and parents is disproportionate. Females are more

closely related to their sisters than they are to their offspring. Between full sisters, the coefficient of relatedness is r > 0.75 (due to their haplodiploid genetic system).[14] Between parent and offspring, the coefficient of relatedness is r = 0.5, because, given the event in meiosis, a certain gene has a 50% chance of being passed on to the offspring. The level of relatedness is an important dictator of individual interactions.



Holes in a tree from carpenter ants

Kin recognition

According to Hamilton's rule for relatedness, for relative-specific interactions to occur, such as kin altruism, a high level of relatedness is necessary between two individuals. Carpenter ants, like many social insect species, have mechanisms by which individuals determine whether others are nestmates or not. They are useful because they explain the presence or absence of altruistic behavior between individuals. They also act as evolutionary strategies to help prevent incest and promote kin selection.[15] Social carpenter ants recognize their kin in many ways. These methods of recognition are largely chemical in nature, and include environmental odors, pheromones, "transferable labels", and labels from the queen that are distributed to and among nest members.[16] Because they have a chemical basis for emission and recognition, odors are useful because many ants can detect such changes in their environment through their antennae.[17] This allows acceptance of nestmates and rejection of non-nestmates.

The actual process of recognition for carpenter ants requires two events. First, a cue must be present on a "donor animal". These cues are called "labels". Next, the receiving animal must be able to recognize and process the cue. In order for an individual carpenter ant to be recognized as a nestmate, it must, as an adult, go through specific interactions with older members of the nest.[16] This process is also necessary in order for the ant to recognize and distinguish other individuals. If these interactions do not occur in the beginning of adult life, the ant will be unable to be distinguished as a nestmate and unable to distinguish nestmates.[18]



Sawdust like shavings from carpenter ants

Kin altruism

Recognition allows for the presence of kin-specific interactions, like kin altruism. Altruistic individuals increase other individuals' fitness at the expense of their own fitness. Carpenter ants perform altruistic actions toward their nestmates so that their shared genes are propagated more readily or more often. In many social insect species like these ants, many worker animals are sterile and do not have the ability to reproduce. As a result, they forgo reproduction to donate energy and help the fertile individuals reproduce.

Pheromones

As in most other social insect species, individual interaction is heavily influenced by the queen. The queen can influence individuals with odors called pheromones, which can have different effects. Some pheromones have been known to calm workers, while others have been known to excite them. Pheromonal cues from ovipositing queens have a stronger effect on worker ants than those of virgin queens.[19]

Social immunity

In many social insect species, social behavior can increase the disease resistance of animals. This phenomenon, called social immunity, exists in carpenter ants. It is mediated through the feeding of other individuals by regurgitation. The regurgitate can have antimicrobial activity, which would be spread amongst members of the colony. Some proteases with antimicrobial activity have been found to exist in regurgitated material. Communal sharing of immune response capability is likely to play a large role in colonial maintenance during highly pathogenic periods.[20]

Polygyny

Polygyny is often associated with many social insect species, and is usually characterized by limited mating flights, small queen size, and other characteristics. However, carpenter ants have "extensive" mating flights and relatively large queens, distinguishing them from polygynous species. Carpenter ants are described as oligogynous because they have a number of fertile queens which are intolerant of each other and must therefore spread to different areas of the nest. Some aggressive interactions have been known to take place between queens, but not necessarily through workers. Queens become aggressive mainly to other queens if they trespass on a marked territory. Queens in a given colony can work together in brood care[5] and the workers tend to experience higher rates of survival in colonies with multiple queens. Some researchers still subscribe to the notion that carpenter ant colonies are only monogynous.[21]

Exploding ants

In at least nine Southeast Asian species of the *Cylindricus* complex, including *Camponotus saundersi*, workers feature greatly enlarged mandibular glands that run the entire length of the ant's body. They can release their contents suicidally by performing autothysis, thereby rupturing the ant's body and spraying toxic substance from the head, which gives these species the common name "exploding ants."[22][23][24] The enlarged mandibular gland, which is many times the size of that of a normal ant, produces a glue. The glue bursts out and entangles and immobilizes all nearby victims.[25][26]

The termite species *Globitermes sulphureus* has a similar defensive system.[27]

Selected species

- *Camponotus aeneopilosus* Mayr, 1862 – golden tail sugar ant
- *Camponotus amaurus* (Espadaler, 1997)
- *Camponotus americanus*
- *Camponotus anderseni*
- *Camponotus atriceps* – Florida carpenter ant (cf. *C. floridanus*)
- *Camponotus bishamon*
- *Camponotus chromaiodes* – red carpenter ant
- *Camponotus cinctellus* – shiny sugar ant
- *Camponotus compressus* (Fabricius, 1787)
- *Camponotus consobrinus* – banded sugar ant
- *Camponotus crassus* Mayr, 1862
- *Camponotus cruentatus* (Latreille, 1802)
- *Camponotus daitoensis*
- *Camponotus detritus* Emery, 1886 – Namib Desert dune ant
- *Camponotus empedocles* – glossy sugar ant
- *Camponotus ferrugineus* – red carpenter ant
- *Camponotus festinatus* (Buckley, 1866)
- *Camponotus flavomarginatus* Mayr, 1862
- *Camponotus floridanus*, Florida carpenter ant, genome 90% sequenced[28]



C. pennsylvanicus, winged male

- *Camponotus haroi* (Espadaler, 1997)
- *Camponotus herculeanus* (Linnaeus, 1758) – Hercules ant
- *Camponotus japonicus* Mayr, 1866 – Japanese carpenter ant
- *Camponotus kaura*
- *Camponotus ligniperda*, a common species in Europe
- *Camponotus modoc* Wheeler, W. M., 1910 – western carpenter ant
- *Camponotus monju*
- *Camponotus nearcticus* (Emery) – smaller carpenter ant
- *Camponotus nigriceps* (Smith, 1858) – black-headed sugar ant
- *Camponotus novaeboracensis*
- *Camponotus pennsylvanicus* (DeGeer) – black carpenter ant
- *Camponotus reburrus* Mackay, in Mackay & Barriga, 2012
- *Camponotus punctulatus* (Mayr) – Tacuru ant
- *Camponotus saundersi*
- *Camponotus schmitzi* Stärke, 1933 – diving ant
- *Camponotus sericeus*
- *Camponotus silvestrii* Emery, 1906
- *Camponotus taino*
- *Camponotus tortuganus* (Emery) – Tortugas carpenter ant
- *Camponotus triodiae*
- *Camponotus universitatis* Forel, 1890
- *Camponotus vagus* Scopoli, 1763
- *Camponotus variegatus* (Smith, F., 1858) – Hawaiian carpenter ant



C. crispulus queen



Wood damage by *C. herculeanus*

Relationship with humans

As pests

Carpenter ants can damage wood used in the construction of buildings. They can leave behind a sawdust-like material called frass that provides clues to their nesting location. Carpenter ant galleries are smooth and very different from termite-damaged areas, which have mud packed into the hollowed-out areas. Carpenter ants can be identified by the general presence of one upward protruding node, looking like a spike, at the "waist" attachment between the thorax and abdomen (petiole). Control involves application of insecticides in various forms including dusts and liquids. The dusts are injected directly into galleries and voids where the carpenter ants are living. The liquids are applied in areas where foraging ants are likely to pick the material up and spread the poison to the colony upon returning.[29]



This structural board was destroyed by carpenter ants. They left the dense "late wood" of each growth ring intact, to use as galleries.

As food

Carpenter ants and their larvae are eaten in various parts of the world. In Australia, the Honeypot ant (*Camponotus inflatus*) is regularly eaten raw by Indigenous Australians.[30] It is a particular favourite source of sugar for Australian Aborigines living in arid regions, partially digging up their nests instead of digging them up entirely, in order to preserve this food source.[31][32] In North America, lumbermen during the early years in Maine would eat carpenter ants to prevent scurvy,[33] and in John Muir's publication, *First Summer in the Sierra*, Muir notes that the Digger Indians of California ate the tickling, acid gasters of the large jet-black carpenter ants.[34] In Africa, carpenter ants are among the vast amount of species that are consumed by the San people.[35]



This structural board was destroyed by carpenter ants. They left the dense "late wood" of each growth ring intact, to use as galleries.



Honeypot ants in Northern Territory, Australia

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External links

- Carpenter Ant Information (http://www.catseyepest.com/pest-library/carpenter-ants)
- University of Kentucky Extension Fact Sheet (http://www.uky.edu/Agriculture/Entomology/entfacts/struct/ef603.htm)
- Ohio State University Extension Fact Sheet (http://ohioline.osu.edu/hyg-fact/2000/pdf/2063.pdf)

- Carpenter Ant Fact Sheet (http://www.pestworld.org/pest-guide/ants/carpenter-ants/) from the National Pest Management Association with information on habits, habitat and prevention
- Carpenter Ants (https://web.archive.org/web/20090705130357/http://gardening.wsu.edu/library/inse004/inse004.htm) An online supplemental to "Carpenter Ants: Biology and Control" by Laurel Hansen, Ph.D. of Spokane Falls Community College

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Fire ant

Fire ant is the common name for several species of ants in the genus ***Solenopsis***. They are, however, only a minority in the genus, which includes over 200 species of *Solenopsis* worldwide. *Solenopsis* are stinging ants and most of their common names reflect this, for example, **ginger ants** and **tropical fire ants**. Many species also are called **red ants** because of their light brown color, though species of ants in many other genera are similarly named for similar reasons. Examples include *Myrmica rubra* and *Pogonomyrmex barbatus*.[2]

None of these names apply in all countries nor to all species of *Solenopsis*, nor only to *Solenopsis* species; for example the colloquial names for several species of weaver ants in the genus *Oecophylla* in Southeast Asia include "fire ants" because of their red color and painful sting; the two genera, however, are not closely related. Also, *Wasmannia auropunctata* is commonly called the "little fire ant".[3]

Fire ant



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	Myrmicinae
Tribe:	Solenopsidini
Genus:	*Solenopsis* Westwood, 1840
Type species	
Solenopsis geminata (Fabricius, 1804)	
Diversity[1]	
201 species	

Contents

Appearance of fire ants

Behavior

Roles

- Queen
- Males (drones)
- Other roles

Invasive species

Symptoms and treatment for fire ant sting

Predators

Species

See also

References

Further reading

External links

Appearance of fire ants

The bodies of mature fire ants, like the bodies of all typical mature insects, are divided into three sections: the head, the thorax, and the abdomen, with three pairs of legs and a pair of antennae. Fire ants of those species invasive in the United States can be distinguished from other ants locally present by their copper brown head and thorax with a darker abdomen. The worker ants are



Fire ant mound

blackish to reddish and their size varies from 2 to 6 mm (0.079 to 0.236 in). In an established nest these different sizes of ants are all present at the same time.[4]



Detail of the head (*Solenopsis geminata*)

Solenopsis spp. ants can be identified by three body features—a pedicel with two nodes, an unarmed propodeum, and antennae with 10 segments plus a two-segmented club.[5] Many ants bite, and formicine ants can cause irritation by spraying formic acid; myrmecine ants like fire ants have a dedicated venom-injecting sting, which injects an alkaloid venom, as well as mandibles for biting.[6]

Behavior



A fire ant worker, queen, and male (clockwise from bottom left)

A typical fire ant colony produces large mounds in open areas, and feeds mostly on young plants and seeds. Fire ants often attack small animals and can kill them. Unlike many other ants, which bite and then spray acid on the wound, fire ants bite only to get a grip and then sting (from the abdomen) and inject a toxic alkaloid venom called solenopsin, a compound from the class of piperidines. For humans, this is a painful sting, a sensation similar to what one feels when burned by fire (hence the name), and the after-effects of the sting can be deadly to sensitive people.[7] Fire ants are more aggressive than most native species, so have pushed many species away from their local habitat. One such species that *Solenopsis* ants parasitically take advantage of are bees, such as *Euglossa imperialis*, a nonsocial orchid bee species, from which the ants would enter the cells from below the nest and rob the cell's contents.[8] These ants are renowned for their ability to survive extreme conditions. They do not hibernate, but can survive cold conditions, although this is costly to fire ant populations as observed during several winters in Tennessee, where 80 to 90% of colonies died due to several consecutive days of extremely low temperatures.[9]

Fire ants have been known to form mutualistic relationships with several species of Lycaenidae and Riodinidae butterflies.[10][11] In *Lycaena rubidus*, the larvae secrete a fluid that is high in sugar content. Fire ants bring the larvae back to the nest, and protect them through the pupal stage in exchange for feeding on the fluid.[11] In *Eurybia elvina*, fire ants were observed to frequently construct soil shelters over later instars of larvae on inflorescences on which the larvae are found.[10]

Fire ants nest in the soil, often near moist areas, such as river banks, pond shores, watered lawns, and highway shoulders. Usually, the nest will not be visible, as it will be built under objects such as timber, logs, rocks, or bricks. If no cover for nesting is available, dome-shaped mounds are constructed, but these are usually only found in open spaces, such as fields, parks, and lawns. These mounds can reach heights of 40 cm (16 in),[4] but can be even higher on heavier soils, standing at 1.0 m (3 ft 3 in) in height and 1.5 m (4 ft 11 in) in diameter.[12] Colonies are founded by small groups of queens or single queens. Even if only one queen survives, within a month or so, the colony can expand to thousands of individuals. Some colonies may be polygynous (having multiple queens per nest).[13]

Fire ants are resilient and can survive floods. During Hurricane Harvey in Texas in 2017, clumps of fire ants, known as rafts, were seen clumped together on the surface of the water. Each clump had as many as 100,000 individual ants, which formed a temporary structure until finding a new permanent home.[14]

Fire ants dig tunnels efficiently using about 30% of the population of the colony, thereby avoiding congestion in tunnels.[15]

Roles

Queen

Fire ant queens, the reproductive females in their colony, also are generally the largest. Their primary function is reproduction. Typically, a fire ant queen will seek to establish a new colony following a nuptial flight, wherein it will use its special venom to paralyse offending competitors,[16] in the absence of workers for defence. Fire ant queens may live up to seven years and can produce up to 1,600 eggs per day, and colonies will have as many as 250,000 workers.[12][17] The estimated potential life span is around 5.83 to 6.77 years.[18] Young, virgin fire ant queens have wings (as do male fire ants), but they rip them off after mating.



Solenopsis winged reproductive females, queens and workers

Males (drones)

The main purpose of the fire ant males is to mate with queens during a nuptial flight. After a male has successfully inseminated a queen , its purpose is fulfilled, he will not get accepted back to the mother colony, and eventually dies outside the nest.[19]

Other roles

The other roles in an ant colony are usually undertaken by workers. Fire ant workers are haphazardly divided into different size classes, namely minima, minor, media, and major workers.[20] The major ants are known for their larger size and more powerful mandibles typically used in macerating and storing food items (i.e. as repletes), while smaller workers take care of regular tasks (the main tasks in a colony are caring for the eggs/larvae/pupae, cleaning the nest, and foraging for food).[12] However, *Solenopsis daguerrei* colonies contain no workers, as they are considered social parasites.[21]

Invasive species

Although most fire ant species do not bother people and are not invasive, *Solenopsis invicta*, known in the United States as the red imported fire ant (or RIFA) is an invasive pest in many areas of the world, notably the United States, Australia, China and Taiwan.[22] The RIFA was believed to have been accidentally introduced to these countries via shipping crates, particularly with Australia when they were first found in Brisbane in 2001.[23] These ants have now since been spotted in Sydney for the first time.[24] They were believed to be in the Philippines, but they are most likely to be misidentified for *Solenopsis geminata* ants.[25]

In the US the FDA estimates that more than US$5 billion is spent annually on medical treatment, damage, and control in RIFA-infested areas. Furthermore, the ants cause approximately $750 million in damage annually to agricultural assets, including veterinarian bills and livestock loss, as well as crop loss.[26] Over 40 million people live in RIFA-infested areas in the southeastern United States.[27] It is estimated that 30–60% of the people living in fire ant-infested areas of the US are stung each

year.[28] RIFA are currently found mainly in subtropical southeastern USA states including Florida, Georgia, South Carolina, Louisiana, Mississippi, Alabama, and parts of North Carolina, Virginia, Tennessee, Arkansas, Texas, Oklahoma, New Mexico, and California.[29]

Since September 2004 Taiwan has been seriously affected by the red fire ant. The US, Taiwan and Australia all have ongoing national programs to control or eradicate the species, but with the exception of those in Australia, none have been especially effective. In Australia, there is an intensive program costing A$175 million, although the fire ant has remained despite efforts.[30] By July 2013 multiple sites west of Brisbane were confirmed, including the Lockyer Valley, Muirlea and Goodna.[31] According to a study published in 2009, it only took seventy years for the lizards in parts of the United States to adapt to the ant's presence – they now have longer legs and new behaviors that aid them in escaping from the danger.[32]



Sign for the Fire Ant Festival in Ashburn, Georgia

Symptoms and treatment for fire ant sting

The venom of fire ants is mainly (>95%) composed of oily alkaloids structurally derived from piperidine (also known as solenopsins) mixed with a small amount of toxic proteins.[33][34] Fire ant stings are painful, characterised by a local burning sensation, followed by urticaria.[33] The sting site typically swells into a bump within hours, which can cause further pain and irritation, especially following several stings at the same place. The bump may develop into a white pustule within 24–36 hours which can become infected if scratched, but will spontaneously flatten within a few days if left alone. The pustules are obtrusive and uncomfortable while active and, if they become infected, may cause scarring.[35] Some people may become allergic to the venom,[36] and if untreated, may become increasingly sensitive to the point of experiencing anaphylaxis following fire ant stings, which requires emergency treatment. Management of an emergency visit due to anaphylaxis is recommended with the use of adrenaline.[37] It has been demonstrated that, whilst pustule formation results from the injected venom alkaloids,[38] allergy to fire ant stings is caused solely by venom allergenic proteins.[36]


A human leg three days after brief contact with a fire ant colony

First aid for fire ant stings includes external treatments and oral medicines. There are also many home remedies of varying efficacy, including immediate application of a solution of half bleach and half water, or aloe vera gel – the latter of which is also often included in over-the-counter creams that also include medically tested and verified treatments.[7] External, topical treatments include the anesthetic benzocaine, the antihistamine diphenhydramine, and the corticosteroid hydrocortisone.[7] Antihistamines or topical corticosteroids may help reduce the itching and will generally benefit local sting reactions.[39] Oral medicine include antihistamines.[40] Severe allergic reactions to fire ant stings, including severe chest pain, nausea, severe sweating, loss of breath, serious swelling, and slurred speech,[41] can be fatal if not treated.[42]

Predators

Phorid flies, or Phoridae, are a large family of small, hump-backed flies somewhat smaller than vinegar flies; two species in this family (*Pseudacteon tricuspis* and *Pseudacteon curvatus*) are parasitoids of the red imported fire ant in its native range in South America. Some 110 species of the genus *Pseudacteon*, or ant-decapitating flies, have been described. Members of *Pseudacteon* reproduce by laying eggs in the thorax of the ant. The first instar larvae migrates to the head, then develops by feeding on the

hemolymph, muscle tissue, and nervous tissue. After about two weeks, they cause the ant's head to fall off by releasing an enzyme that dissolves the membrane attaching the ant's head to its body. The fly pupates in the detached head capsule, emerging two weeks later.[43]

Pseudacteon flies appear to be important ecological constraints on *Solenopsis* species and they have been introduced throughout the southern United States, starting with Travis, Brazos, and Dallas counties in Texas, as well as south central Alabama, where the ants first entered North America.[44]



Venus flytrap



Pseudacteon curvatus, phorid fly parasitoid of fire ants

The Venus flytrap, a carnivorous plant, is native only to North and South Carolina in the United States. About 33% of the prey of the Venus flytrap are ants of various species.[45] They lure their prey with a sweet sap. Once the prey has entered the trap and within about three seconds has touched two or three "trigger hairs", bristles on the surface of the trap, the leaf closes around the prey, confining it behind the "teeth" on its perimeter, and digests it. The majority of ants that are captured include non-native RIFAs, and three other species of ants.[45] Other carnivorous plants, such as sundews (*Drosera*) and various kinds of pitcher plants also trap many ants.



A species of *Drosera* with its sticky leaves that trap many ants

Key natural enemies of fire ants also include other ant species which will attack prospective queens during the nest founding period, when there is an absence of workers to defend the emergent colony.[46] Frequent competitors of fire ant founding queens include other *Solenopsis* thief ant species, and some invasive pest species, such as the tawny crazy ant, and the black crazy ant.[16]

A number of entomopathogenic fungi are also natural enemies of fire ants, such as *Beauveria bassiana*[47] and *Metarhizium anisopliae*[48]. The latter is commercially available for the biological control (i.e. pesticide-free) of various pest insects, and a new proposed technology has increased its shell life and efficiency of against fire ants. [49]

Species

The genus *Solenopsis* contains over 200 species.[1] Not all species included in the genus are known as fire ants, but most are small slow-moving ants which are unable to sting, called thief ants. "True" fire ants are but a group of about 20 species of *Solenopsis* which are larger, and will viciously sting in swarms whenever disturbed.[50] Some of the most studied species include:

- *Solenopsis invicta* Buren, 1972
- *Solenopsis richteri* Forel, 1909
- *Solenopsis saevissima* (Smith, 1855)
- *Solenopsis silvestrii* Emery, 1906
- *Solenopsis solenopsidis* (Kusnezov, 1953)
- *Solenopsis xyloni* McCook, 1879
- *Solenopsis geminata* (Fabricius, 1804)

See also

- Ant stings
- Ant venom
- Ants of medical importance
- Bullet ant
- Red imported fire ants in Australia

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Further reading

- Bert Hölldobler and Edward O. Wilson (1990). *The Ants*. Cambridge: Belknap Press of Harvard University Press. ISBN 978-3-540-52092-4.

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Tapinoma sessile

Tapinoma sessile is a species of small ant that goes by the common names **odorous house ant**, **sugar ant**, **stink ant**, and **coconut ant**.[1] Their colonies are polydomous (consist of multiple nests) and polygynous (contain multiple reproducing queens). Like many social insects, *T. sessile* employs complex foraging strategies, allocates food depending on environmental conditions, and engages in competition with other insects.[2][3][4]

T. sessile can be found in a huge diversity of habitats, including within houses. They forage mainly for honeydew, which is produced by aphids and scale insects that are guarded and tended by the ants, as well as floral nectar and other sugary foods. They are common household pests and are attracted to sources of water and sweets.[3][5][6]

As with most other ants, *T. sessile* is eusocial. This is characterized by reproductive division of labor, cooperative care of the young, and overlapping generations.[6][7]

Tapinoma sessile	
	
Tapinoma sessile worker	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	Dolichoderinae
Genus:	*Tapinoma*
Species:	***T. sessile***
Binomial name	
Tapinoma sessile Say, 1836	

Contents

Etymology

Description

Distribution

Behavior

- Food allocation
- Seasonal behaviors
- Competition with other ants
- Other habits

Predators and parasites

Pest control

References

External links

Etymology

The binomial name *Tapinoma sessile* was assigned by Thomas Say in 1836. *Sessile* translates to "sitting" which probably refers to the gaster sitting directly on top of the petiole in the abdomen of the ant species.[8] The common names "odorous house ant" and "coconut ant" come from the odor the ants produce when crushed, which is very similar to the pungent odor of a rotting coconut, blue cheese, or turpentine.[1]

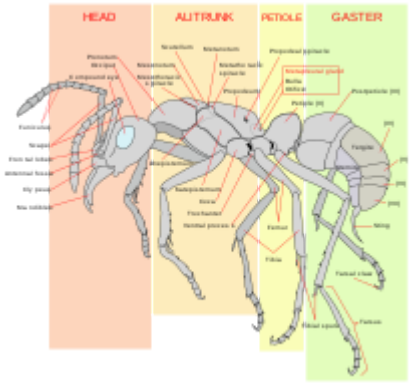
Description

T. sessile is a small ant that ranges in color from brown to black, and varies in length from $^{1}/_{16}$ to $^{1}/_{8}$ inches (1.5–3.2 mm). When crushed, these ants leave a smell which leads to their nickname "stink ant".[1][5][6]

The gaster portion of the abdomen sits directly on top of the petiole in the abdomen of this species, which helps distinguish them from other small, dark, invasive ants.[8] A comparison of the side view of the *T. sessile* (below) and a diagram of the a typical ant body (below) shows how the *T. sessile*'s gaster sits atop its petiole. This leads to a very small petiole and to the gaster being pointed downward. The anal pore then opens ventrally (toward the abdomen) instead of distally.[8]



A side view of the body of a *T. sessile*. It shows that the gaster part of the abdomen is directly above the ant's petiole.



A diagram showing the names of the different sections of a typical ant's body. Note that the petiole in this "typical ant" is in front of the gaster, rather than under it.



The antennae of the *T. sessile* has 12 distinct segments

Their antennae have 12 segments.[6]

The queens lay the eggs which incubate between 11–26 days. After hatching, the larval stage lasts between 13–29 days, and the pre-pupal and pupal stages last between 10–24 days.[6] Little is known about the lifespan of the ant, though it has been shown that queens live at least 8 months (and probably much longer), workers at least a few months (and show every indication of living as long as queens), while males appear to live only approximately a week.

Distribution

T. sessile is native to North America and ranges from southern Canada to northern Mexico, but is less common in the desert southwest.[6]

Behavior

Colonies vary in size from a few hundred to tens of thousands of individuals. Big colonies usually have multiple queens.[6]

The odorous house ant is tough: Injured workers have been observed to continue living and working with little hindrance, some queens with crushed abdomens still lay eggs, and there are documented instances of *T. sessile* queens surviving without food or water for over two months. They also appear highly tolerant to heat and cold. These ants are difficult to remove from a home after their colony has become well-established.[5]

When offered a choice of food sources, the ants preferred sugar and protein over lipids, and this preference persisted in all seasons. When specific sugar sources were studied the ants preferred sucrose over other sugars, such as fructose or glucose.[3]

Food allocation

Foragers collect food that is around the nest area and bring it back to the colony to share with the other ants. *T. sessile* has polydomous colonies, meaning that one colony has multiple nests. Because of this, *T. sessile* is very good at foraging for food when there is great variance in the distribution of resources. Instead of going back to a faraway nest to deliver food, they move workers, queens, and the brood to be closer to the food, so that they can reduce the cost in effort of food transport. This is called 'dispersed central-place foraging'.[2] It was also found that the half-life of the stay at any one nest was about 12.9 days.[9]

Buczkowski and Bennett also studied the pattern of food movement within a nest. They labeled sucrose with Immunoglobin G (IgG) proteins, and then identified them using an enzyme-linked immunosorbent assay (ELISA) to track the movement of food. They found that food was spread through *trophallaxis* (one animal regurgitating food for another). Despite this trophallactic spread of food, the workers kept most of the sucrose. They also found that some queens received more food than others, suggesting a dominance hierarchy even between queens. They also found that the nests were located in a system of trails, and that their distribution depended on where food was found and the distance between these patches of food.[2] It was also found that the rate of trophallactic feeding depends on the number of ants per nest, and the quality of food available. When the number of donors is kept constant, but the number of total individuals in increased, more individuals test positive for the food marker. This indicates that more individuals are eating, but the amount they eat is less. If the number of donors was doubled, and the size of the overall population increased, the number of individuals receiving food more than doubled, again indicating that the number of individuals fed increased, but that the per capita amount of food consumed decreased.[10]

When searching for food, primary orientation is when ants are exploring a new terrain without the guidance of odor trails. Secondary orientation is when terrain has been explored, and there are pre-existing odor trails which ants use to orient themselves. When *T. sessile* ants are orienting themselves for the first time they often rely on topography. The major types of elements they rely on are bilaterally elevated, bilaterally depressed, unilaterally elevated, and unilaterally depressed. They use these types of surfaces to orient along, and lay the first odor trails, which can then be followed in the future, to the food source, by other ants.[11]

Seasonal behaviors

It was also found that this ant species practices seasonal *polydomy* (having multiple colony sites) to have access to multiple food sources. The colony will overwinter in a single nest, and then during spring and summer when resources are more abundant they will form multiple nests. This allows them to better use food sources, that might be spread out. During the winter they will return again to the same nest location. Seasonal polydomy is rather rare, and only found in 10% of all polydomous species.[12] Seasonal polydomy is not found in many ant species, but there are many ant species, including *T. sessile*, which move within a season: Migration to better forage sites is common.[9]

Seasonal activity patterns of the ants were also studied, and corresponding to the seasonal polydomy, it was observed that the ants displayed the most activity between March and September and displayed almost no activity from October to December. Daily activity patterns were also studied. In March *T. sessile* foraged during the day, but in April that pattern changed and the ant began to forage during both day and night. During most of the summer, *T. sessile* shows low levels of activity throughout the day and night.[13]

Competition with other ants

Competition between species is often classified as exploitation or interference. Exploitation involves finding and using limited resources before they can be used by other species, while interference is the act of preventing others from getting resources by more direct force or aggression. When it comes to these behaviors, a species is considered *dominant* if it initiates an attack and

subordinate if it avoids other species. In comparison with eight other ant species, the *T. sessile* was more subordinate on the dominant to subordinate scale. The ant does not show a large propensity for attack, preferring to use chemical secretions instead of biting.[4]

When the *T. sessile*, a subordinate species, was in the presence of dominant ant species such as *C. ferrugineus*, *P. imparis*, *Lasius alienus*, and *F. subsericea*, they reduced the amount of time spent foraging. This was tested with the use of bait, and when the subordinate species, such as *T. sessile*, encountered a dominant species they would leave the bait. It would then make sense that the subordinate species would forage at a different time than dominant species, so that they could avoid confrontation, but there is sizable overlap in foraging period on a daily and seasonal basis. Because the *T. sissile* forages at the same time as dominant species, but avoids other foraging ants, they must have excellent exploitative abilities to survive.[13]

One of the invasive species that *T. sessile* has had to contend with is the Argentine ant, *Linepithema humile*. Studies of its interactions with *L. humile* has helped researchers better understand the aggression of *T. sessile*. *T. sessile* ants rarely fight alongside their nest-mates: They only were observed to have fought collectively in six of forty interactions. This often caused *T. sessile* to lose altercations with other ant species, such as the *L. humile*, even when more *T. sessile* individuals were present. Whereas other ant species like *L. humile* fight together, the *T. sessile* do not. The *T. sessile* is however more likely to win in one-on-one interactions because they have effective chemical defenses.[14]

Other habits

This species is a scavenger / predator ant that will eat most household foods, especially those that contain sugar, as well as other insects. Indoors they will colonize near heat sources or in insulation. In hot and dry situations, nests have been found in house plants and even in the lids of toilets. Outdoors they tend to colonize under rocks and exposed soil. They appear, however, to form colonies virtually anywhere, in a variety of conditions.

In experiments where *T. sessile* workers were confined in an area without a queen, egg-laying (by the workers) was observed, though the workers destroyed any prepupa that emerged from the eggs.[5]

Odorous house ants have been observed collecting honeydew to feed on from aphids, scale insects, and membracids.

They appear to be more likely to invade homes after rain (which washes away the honeydew they collect).

Odorous house ants appear to be highly tolerant of other ants, with compound nests consisting of multiple ant species that included *T. sessile* having been observed.

Predators and parasites

Some birds and toads will eat odorous house ants on occasion.

Wheeler (1916) mentions *Bothriomyrmex dimmocki* as a possible parasite of odorous house ant colonies, suggesting that *B. dimmocki* queens invade and replace *T. sessile* queens.

Isobrachium myrmecophilum (a small wasp) appears to parasitize odorous house ants.

Pest control

T. sessile are not hard to control; they are vulnerable to most ant-killers, which are especially effective when applied as soon as their presence is noticed. If dealt with early, their numbers can be brought under control in just a few days. However, the longer a colony is ignored, the larger the population becomes and the longer it will take to clear the infestation – possibly a few weeks.[5] These ants most commonly invade buildings in late winter and early spring (particularly after rain), at which times one should be on the lookout for newly-arrived ants foraging indoors.[6][9]

To discourage immigration, standing water should be eliminated in the house, as *T. sessile* are attracted to moisture.[3] Plants should be trimmed away from buildings, so they do not make convenient routes for above-ground entry. Cracks, holes and joints should be sealed with polyurethane foam or caulk, especially those that are near the ground. Firewood, rocks, and other materials should not be stored next to a home because it provides sites for nest building near the home, and *T. sessile* naturally relocate their colonies to be near successful forage sites.[6][12][2]

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External links

- Media related to *Tapinoma sessile* at Wikimedia Commons

- "Odorous house ants" (http://www.pestworld.org/pest-guide/ants/odorous-house-ants/). Fact Sheet. National Pest Management Association. – data highlighting habits, habitats and threats

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Pharaoh ant

The **pharaoh ant** (*Monomorium pharaonis*) is a small (2 mm) yellow or light brown, almost transparent ant notorious for being a major indoor nuisance pest, especially in hospitals.[1] The pharaoh ant, whose origins are unknown, has now been introduced to virtually every area of the world, including Europe, the Americas, Australasia and Southeast Asia. It is a major pest in the United States, Australia, and Europe.[2][3]

This species is polygynous, meaning each colony contains many queens, leading to unique caste interactions and colony dynamics. This also allows the colony to fragment into bud colonies quickly.

Pharaoh ants are a tropical species, but they thrive in buildings almost anywhere, even in temperate regions provided central heating is present.

Pharaoh ant



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	Myrmicinae
Tribe:	Solenopsidini
Genus:	*Monomorium*
Species:	***M. pharaonis***

Binomial name

Monomorium pharaonis
(Linnaeus, 1758)

Synonyms

Formica pharaonis
Myrmica pharaonis

Contents

Physical characteristics
Life cycle
Colony proliferation
Pheromones
Foraging
- Trails
- Feeding

Caste system
Nest demographic
Reproduction
Queen–worker relationship
Colony interaction
Washing
Invasiveness and extermination
See also
References
External links

Physical characteristics

Pharaoh workers are about 1.5 to 2 millimeters long, a little more than 1/16-inch. They are light yellow to reddish brown in color with a darker abdomen. Pharaoh ant workers have a non-functional stinger used to generate pheromones.[4] The petiole (narrow waist between the thorax and abdomen) has two nodes and the thorax has no spines. Pharaoh ant eyesight is poor and they possess on average 32 ommatidia.[5] The antennal segments end in a distinct club with three progressively longer segments.

Males are about 3mm long, black, winged (but do not fly). Queens are dark red and 3.6–5mm long. They initially have wings that are lost soon after mating, but do not fly.[6]



A pharaoh ant worker near the tip of a ball point pen

Life cycle

The pharaoh ant queen can lay hundreds of eggs in her lifetime. Most lay 10 to 12 eggs per batch in the early days of egg production and only four to seven eggs per batch later. At 27 °C (80 °F) and 80 percent relative humidity, eggs hatch in five to seven days. The larval period is 18 to 19 days, pre-pupal period three days and pupal period nine days. About four more days are required to produce sexual female and male forms. From egg to sexual maturity, it takes the pharaoh ant about 38 to 45 days, depending on temperature and relative humidity. They breed continuously throughout the year in heated buildings and mating occurs in the nest. Mature colonies contain several queens, winged males, workers, eggs, larvae, pre-pupae and pupae.[3]

Colony proliferation

Each colony produces sexually reproductive individuals roughly twice a year. However, colonies raised in a laboratory can be manipulated to produce sexuals at any time of year. Colonies proliferate by "budding"[3] (also called "satelliting" or "fractionating"), where a subset of the colony including queens, workers and brood (eggs, larvae and pupae) leave the main colony for an alternative nest site.

Pharaoh ant colonies appear to prefer familiar nests to novel nests while budding. This suggests the ability for colonies to remember certain qualities of their living space. However, if the novel (unfamiliar) nest is of superior quality, the colony may initially move toward the familiar, but will eventually select the unfamiliar. The colony assumes the familiar nest is preferable, unless they sense better qualities in the novel nest. This decision-making process seeks to minimize the time the colony is without a nest while optimizing the nest the colony finally chooses.[7]

The number of available budding locations has a large effect on colony fragmentation. A large number of bud nests results in small colony fragments, indicating that the colony has the ability to control size and caste ratios. However, a minimum group size of 469 individuals appears preferred by the species. Amount of fragmentation does not have an effect on food distribution. After budding, nest units do not compete for resources, but rather act cooperatively. This is evolutionarily explained by the high amount of genetic relatedness among these nest units. In addition, major disturbances to the central nest cause the colony to abandon it and flee to a bud nest. Thus, nest units may exchange individuals after budding occurs, further explaining their cooperative behavior.[8]


Monomorium pharaonis worker with single sugar crystal

In Australia, *Monomorium* species is particularly successful. This fact is particularly curious because of the presence of a very aggressive ant family, *Iridomyrmex*, which is quite proficient at interference competition. *Iridomyrmex* ants are able to quickly seek out food sources and prevent other ant species from reaching them. However, unlike other ant species, *Monomorium* species, despite their unaggressive nature and small size, are able to thrive even in areas where *Iridomyrmex* dominates. This success can be attributed to their efficient foraging strategy, and their novel use of venom alkaloids, repellant chemical signals. With these two behaviors, *Monomorium* species can rapidly monopolize and defend food sources.[9]

Pheromones

Pharaoh ants utilize 3 types of pheromones. One is a long-lasting attractive chemical that is used to build a trail network. It remains detectable even if the ants do not use the trail for several days. Pharaoh ants cease activity at night and begin each day of work at around 8 am, yet parts of the trail network are identical each day.[10] The second pheromone is also attractive, but will decay to imperceptible amounts in a matter of minutes without reapplication. This pheromone is useful in marking food sources, as these are unpredictable and the colony must be able to respond to environmental changes quickly. Individuals will not waste their time on an unprofitable trail route. The third pheromone is a repellant.[11] Pharaoh ants were the first species found to use a negative trail pheromone. If an individual finds an unprofitable area with little food or significant danger, it will release this repellant pheromone, which will warn others and cause them to look elsewhere. While positive pheromones indicating lucrative foraging sites are very common in social insects, the pharaoh ant's negative pheromone is highly unusual.[12] Like the food source marker, the negative pheromone is volatile, decaying roughly two hours after being emitted. It may even be insecticidal in some cases.[10] It is so powerful that an individual can detect it from 30 millimetres (1.2 in) away. Pharaoh ants utilize this pheromone near forks in the trail network, and an ant that detects it will begin to walk in a zigzag manner.[11]

Both the attractive and repellent pheromones are utilized in the decision-making an ant must make while foraging. The repellent pheromone is especially useful in the repositioning of trails after a new food source has been introduced. It also helps prevent ants from concentrating on an undesirable trail. Thus, the repellant pheromone makes the pharaoh ant a particularly efficient forager.[13] Despite their extreme importance, there is an adaptive value to using pheromones sparingly, as it streamlines communication during important decision-making situations, such as a nest migration.[14]

Foraging

Pharaoh ants use a positive feedback system of foraging. Each morning, scouts will search for food. When one finds it, it will instantly return to the nest. This causes several ants to follow the successful scout's trail back to the food source. Soon, a large group will be upon the food. Scouts are thought to use both chemical and visual cues to remain aware of the nest location and find their way.[15] If the colony is exploring a new region, they employ a land rush tactic, in which a large number of foragers randomly search, constantly releasing pheromones.[10]

Even though *M. pharaonis* is most often thought an indoor pest, foraging has been found to be more prevalent outside. Even inside colonies were found to forage close to windows, indicating a propensity for outdoor environment.[1]

Trails

Even though scouts search independently, they use a distinct trail system that remains somewhat constant from day to day. The system consists of one to four trunk routes. Every scout uses one of these trunks in the beginning and end of its food search. In this way, the trunks get continuous chemical reinforcement and do not change much. Each trunk divides into many branch routes. These will change based on food availability.[15]

The organization of foraging trails is strongly affected by the health of the colony and the availability of food. Food deprivation induces a higher amount of foraging ant traffic, compared to a non-deprived population. If a food source is presented to the food deprived colony, this traffic was further increased, an indication of the pharaoh ant's recruitment tactic. If food is not present, a colony will extend its trails to a wider radius around the nest. Logically, number of trails and forager traffic is largest near a food source.[16]

While pheromones explain the pharaoh ant's foraging ability, each forager's capability to find its way back to the nest requires a different explanation. In fact, the pharaoh ant relies on geometry to show it the way home. Each fork in the trail system spreads at an angle between 50 and 60 degrees. When returning to the nest, a forager that encounters a fork will almost always take the path that deviates less from its current direction. In other words, it will never choose an acute angle that would drastically change its

direction. Using this algorithm, each forager is able to find its way back to the nest. If the fork angle is experimentally increased to an angle between 60 and 120 degrees, *M. pharaonis* foragers were significantly less able to find their nest. This method of decision-making reduces the wasted energy that would result from traveling in the wrong direction and contributes to the pharaoh ant's efficiency in foraging.[17]

Feeding

Upon scouts' return with food, the queens will attempt to beg for their share. Depending on food availability and each individual's condition, a scout may refuse the queen's entreaties and even run away from her.[18] The decision of an individual to give up food to the queen may be beneficial in situations of plentiful food, as a healthy queen can reproduce and propagate the colony's genes. However, when food is highly scarce, an individual's own survival can outweigh this potential benefit. She will therefore refuse to give up food.

A queen may also feed on secretions from larvae. This creates a positive feedback loop in which more larvae will provide more food to queens who can in turn produce more larvae.[19]

If a large amount of larvae results in a surplus of secretions, pharaoh ants will store the excess in the gasters of a unique caste, the replete workers. Members of this group have enormous gasters and can regurgitate their stored food when needed. In this way, the colony has a cushion against food shortages.[20]

Pharaoh ants have a sophisticated strategy for food preference. They implement two related behaviors. The first is known as satiation. The workers will at first show a strong preference for a particular food type. However, if this food is offered alone, with no other options, for several weeks, workers will afterward show a distinct preference for a different type of food. In this way, the ants become satiated on a certain food group and will change their decision. The second behavior is called alternation. If given the continuous choice between food groups, pharaoh ants will tend to alternate between carbohydrate-rich foods and protein-rich foods. These satiation and alternation behaviors are evolutionarily adaptive. The decision to vary the type of food consumed ensures that the colony maintains a balanced diet.[21]

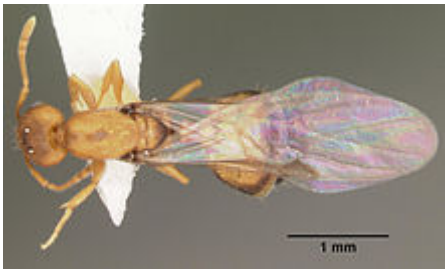
Caste system

Monomorium pharaonis, similar to other invasive ants, is polygynous, meaning its colonies contain many queens (up to 200). It is hypothesized that polygyny leads to lower levels of nestmate recognition in comparison to monogynous species due to the expected higher levels of genetic diversity. Because these colonies lack nestmate recognition, there is no hostility between neighbouring colonies, which is known as unicoloniality.[22]

Many invasive ants display unicoloniality. The adaptive value of this nonaggression among colonies has to do with avoiding unnecessary injury and allowing proper resource allocation, ensuring success for all the colonies. Low nestmate recognition, caused in part by polygyny, also has a biochemical basis in *M. pharaonis*. Cuticular hydrocarbons are compounds, often found on antennae, that allow for communication in many social insects. In ant species, these compounds play an especially key role in nestmate recognition. Differences in cuticular hydrocarbons are detected by other ant species, who respond accordingly. However, all pharaoh ant colonies have the same hydrocarbons on their antennae. This leads to ineffective nestmate recognition, and nonaggression between colonies.[22]

Pharaoh ant colonies contain many queens. The ratio of queens to workers is variable and dependent on the size of the colony. An individual colony normally contains 1,000–2,500 workers, but often a high density of nests gives the impression of massive colonies. In a small colony, there will be more queens relative to workers. In addition, individuals will be larger than those in a more populous colony.[23] This ratio is controlled by the workers in the colony. Larvae that will produce workers have characteristic hairs all over them, while larvae that will produce sexual males or females are bare. It is thought that workers can use these distinguishing features to identify larvae. Workers may cannibalize larvae in order to ensure a favorable caste ratio. This

decision to cannibalize is largely determined by the present caste ratio. If plenty of fertile queens are present, for example, the workers may eat sexual larvae. The caste ratios are controlled in an attempt to maximize the growth of the colony.[24] For example, in a small colony, the ratio of queens to workers is increased. This in turn increases the potential for reproduction, allowing colony growth. Conversely, in a large colony, the high worker to queen ratio maximizes the foraging capacity of the nest, helping sustain the population size.[23]



Dorsal view of an alate pharaoh ant

Nest demographic

The Pharaoh ant is a polygynous species that has a relatively low worker to queen ratio of around 12.86. This allows the pharaoh ants to be able to exert social control over the size of the colony and the size of each caste. In the average nest, there are around 170 ± 8 queens every nest, which comprises around 5.2% of the total population, whereas there are around 2185 ± 49 workers, which make up around 66.6% of the population. This low worker to queen ratio is usually associated with swift changes in the nest and may be why pharaoh ants form many new nest buds quickly.[25] To branch out and form a new bud nest, pharaoh ants need a minimum of 469 ± 28 individuals, which explains how they proliferate so quickly.[26]

Reproduction

Mating for pharaoh ants occurs within the nests with males that are usually not from the colony which ensures genetic diversity. The queen can typically produce eggs in batches of 10 to 12 at once, but can lay up to 400 eggs every time she mates. The eggs that are produced take up to 42 days to mature from an egg to an adult. Each queen within the nest lives between 4 and 12 months.[27]

During copulation, sperm is transferred from male to female inside a spermatophore. There are several theories regarding the adaptive value of using a spermatophore. It contains certain chemicals that may inhibit the female's sex drive. Alternatively, it may physically plug the female's gonophore. In either explanation, the spermatophore prevents the female from reproducing with another male. In essence, the use of a spermatophore is evolutionarily favorable because it increases the probability of the male's genetic code being transferred to subsequent generations by lessening potential competition from other males.[28]

Pharaoh ant copulation, like that of many social insects, is harmful to the female. The penis valve contains sharp teeth, which latch onto a thick, soft cuticular layer in the female. This method of copulation too has an evolutionary basis. The teeth ensure sex lasts long enough for sufficient sperm transfer. Also, the pain caused to the female may, in some ways, lessen her desire to mate again.[28]

Queen–worker relationship

When the queen ant first moves to a new nest, she will rear the first group of workers. Once a worker threshold has been reached, resources will then be invested into new males and queens. When a new nest is formed, queens are not a necessity; workers can raise new queens after finding a suitable nest site.[23][26]

In pharaoh ant colonies new males and queen ants can be produced when the existing fertile queen is removed. When queens are absent, the workers in the nest can do two things: either rear existing sexual larvae or transport sexual larvae from other bud nests or from the main nest to its own nest. However, when there are fertile queens still within the nest, the worker ants will cannibalize the sexual larvae and will either reject or consume sexual larvae from other nests. On the other hand, the worker ants will always accept and nurture worker larvae from other nests.[24][29] Furthermore, according to Schmidt et al., polygamous species such as pharaoh ants will have higher resource allocations towards the female caste instead of the worker caste to ensure rapid growth of new budding colonies.[23]

Colony interaction

When social ants encounter ants from another colony, behavior can be either aggressive or non-aggressive. Aggressive behavior is very commonly seen; the attacking worker usually bites the opponent at the petiole. In non-aggressive behavior, antennation occurs when the two ants meet. In the case of *Monomorium pharaonis*, behavior is almost always non-aggressive even when the ants are from different colonies and of different castes.[30] Very few cases exist where aggressive behavior is seen in these ants.

Washing

After foraging, pharaoh ants will wash themselves when a worker enters the cell. Pharaoh ants will also wash after a long feed. It has been proposed that washing has a hygienic value, keeping the nest area clean, staving off disease and disorder. Right before workers leave to forage, they also may wash themselves. However, in this instance the behavior is extremely violent, often causing the ants to fall over. It is thought that here, the washing behavior has no hygienic value and instead may be a displacement activity, a sign that the ants are deliberating whether or not to exit the nest.[18]

Invasiveness and extermination

Budding is a major factor underlying the invasiveness of pharaoh ants. A single seed colony can populate a large office block, almost to the exclusion of all other insect pests, in less than six months. Elimination and control are difficult because multiple colonies can consolidate into smaller colonies during extermination programs only to repopulate later.

Pharaoh ants have become a serious pest in almost every type of building. They can feed on a wide variety of foods including grease, sugary foods, and dead insects. They can also gnaw holes in silk, rayon and rubber goods. Nests can be very small, making detection even more difficult.[2] They are usually found in wall voids, under floors, or in various types of furniture.[2] In homes, they are often found foraging in bathrooms or near food.[3]

It is recommended not to attempt extermination using insecticidal sprays and dusts because they will cause the pharaoh ants to scatter and colonies to split, although non-repellent residual insecticides have been reported to be effective.[31]

The recommended method to eliminate pharaoh ants is by the use of baits attractive to the species. Modern baits use insect growth regulators (IGRs) as the active substance; the ants are attracted to the bait by its food content, and take it back to the nest. Over a period of weeks the IGR prevents the production of worker ants and sterilizes the queen. Renewing the baits once or twice may be necessary.[31]

Pharaoh and other ants have also been exterminated with baits of 1% boric acid and sugar water.[32]

See also

- Argentine ant, another known pest species

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External links

- Picture of a *M. pharaonis* (http://www.ipm.ucdavis.edu/PMG/M/I-HY-MPHA-AD.001.html)
- Ohio State University Extension Fact Sheet (https://archive.is/20010425022043/http://ohioline.osu.edu/hyg-fact/2000/2136.html) at Archive.today (archived 2001-04-25)
- Pharaoh ant (http://entomology.ifas.ufl.edu/creatures/urban/ants/pharaoh_ant.htm) on the UF / IFAS Featured Creatures Web site

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Solenopsis molesta

Solenopsis molesta is the best known species of *Solenopsis* **thief ants.** These ants, which include the majority of species within the genus *Solenopsis*, get their names from their habit of nesting close to other ant nests, from which they steal food. They are also called grease ants because they are attracted to grease. Nuptial flight in this species occur from late July through early fall.[1]

Solenopsis molesta



Solenopsis molesta worker

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	Myrmicinae
Tribe:	Solenopsidini
Genus:	*Solenopsis*
Species:	***S. molesta***

Binomial name

Solenopsis molesta

Buren, 1972

Contents

Appearance
Distribution
Habitat
Behavior
Mating
Diet
Pest
References
External links

Appearance

S. molesta range anywhere from 1/32 of an inch (0.5 mm) to 1/8 of an inch (3 mm) long. Queens in this species measure at just over 5mm in length and range from a yellow to a light brown color. Workers are yellow and occasionally pale brown in appearance. They have very small eyes and are covered in erect and sub-erect yellow hairs. These ants have a two-segmented petiole (a petiole and postpetiole) connecting their abdomen to the thorax. They have 10 segments in their antennae, which end in large segmented clubs. Thief ants possess small stingers on their oblong abdomens. Worker ants have large jaws for carrying food, usually other ants' brood, back to the colony. The larvae of thief ants have been described from the Brazilian species *Solenopsis helena*.[2] Despite a general resemblance to the larvae of the larger fire ants,[3] the larvae of thief ants are much smaller and present spiculate hairs on their face.[2]

Distribution

S. molesta are native to the United States and can be found in Eastern, Western, and Central parts of the country and northern Mexico.

Habitat



Magnified shot of Solenopsis molesta - Cincinnati, Ohio

The habitat of *Solenopsis molesta* is vast, because they can survive just about anywhere. They can live in people's homes, in the cracks or under the floorboards. They can build nests anywhere, but usually near the nests of other species they steal from. They usually nest under rocks, in any exposed soil, or rotting logs. If they cannot find any of these things, then they move into another colony. Their nests are generally large for the ants' size, and have tunnels that lead to another ant colony for a reliable and steady food source.

Behavior

Colonies of *S. molesta* usually have anywhere from a few hundred to a few thousand workers. Colonies are occasionally polygynous, with a maximum of eight queens in a single nest. The number of thief ants in a colony depends on the location. Colonies with a reliable and ready food source don't have as many workers because food is readily available. Since ants of this species are so small, they can colonize just about anywhere. They can live in people's homes without them ever knowing that they have an infestation of tiny ants. *Solenopsis molesta* are common in homes, and due to their small size they can easily enter sealed packages of food. Other thief ant colonies are inside other ant colonies. They then eat the food and sometimes larva of the host ants. They will eat just about anything, including dead animals and fungal spores, and will travel great distances in search for food. Once food has been found, a trail is formed from the colony to the food so the other thief ant workers can find it.

Mating

S. molesta queens are bigger than the workers, being four to five millimeters long. Mating takes place from July to late fall. Both the queens and *S. molesta* drones have wings, and mating takes place while flying. Queens sometimes fly with a worker or two clinging to their bodies, presumably to help out right away when the queen finds a suitable place for a colony. Queens can lay anywhere from 27 and 387 eggs per day, but the average number of eggs laid per day is 105. It takes about 52 days for an egg to become a fully mobile worker. Young *Solenopsis molesta* spends about 21 days in the larval stage when the weather is suitable.

Diet

They eat grease whenever they find it, which is why they are sometimes called grease ants. They also eat meat, cheese and other dairy products, and seeds. They also eat larvae and pupae of other ant species such as codling moths. Thief ants do not appear to be attracted to sweets, unlike most other ants. They will however, for example, consume fruits and sugary soft drinks.

Pest

Solenopsis molesta can be troublesome when they get into human dwellings. It is extremely hard to find these ants, due to their inaccessible and remote nesting areas and their extremely small size. They are also not always present outside their colony, and travel far to find food. Also, they are so small they can get into things that other insects cannot get into. The easiest way to locate a colony is to look for trails of ants. It is also hard to get rid of a *S. molesta* infestation because they are not attracted to common ant traps. One of the most common ways to get rid of the ants is to put oil or grease in the middle of the ant trap. However, this is a hit-or-miss method, because too little grease will not attract the ants, and too much will limit the effectiveness of the trap. The ants also appear to be resistant to most insecticides. *Solenopsis molesta* are sometimes mistaken for the pharaoh ant, because there are similarities between the two. They are both around the same size, but there are differences in their markings.

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- http://animaldiversity.ummz.umich.edu/site/accounts/classification/Solenopsis_molesta.html#Solenopsis%20molesta

External links

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Cimex

Cimex is a genus of insects in the family Cimicidae.[1] *Cimex* species are ectoparasites that typically feed on the blood of birds and mammals. Two species, *Cimex lectularius* and *Cimex hemipterus*, are known as bed bugs and frequently feed on humans, although other species may parasitize humans opportunistically.[2] Species that primarily parasitize bats are known as bat bugs.

The insects are 3 to 9 millimetres (0.12 to 0.35 in) long and have flattened reddish-brown bodies with small nonfunctional wings.[1]

Bed bugs



Cimex lectularius

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hemiptera
Family:	Cimicidae
Genus:	*Cimex* Linnaeus, 1758

Species

- *Cimex adjunctus*
- *Cimex antennatus*
- *Cimex brevis*
- *Cimex columbarius*
- *Cimex emarginatus*
- *Cimex incrassatus*
- *Cimex japonicus*
- *Cimex latipennis*
- *Cimex lectularius*
- *Cimex hemipterus* (*C. rotundatus*)
- *Cimex pilosellus*
- *Cimex pipistrelli*

Contents

Description

Taxonomy

Feeding habits
- Feeding physiology

Reproduction
- Sperm protection
- Sperm and seminal fluid allocation
- Egg production
- Alarm pheromones

Life stages

Sexual dimorphism

Host searching

Aggregation and dispersal behavior

References

Description

Adult *Cimex* are light brown to reddish-brown, flat, oval, and have no hind wings. The front wings are vestigial and reduced to pad-like structures. Bed bugs have segmented abdomens with microscopic hairs that give them a banded appearance. Adults grow to 4–5 mm (0.16–0.20 in) long and 1.5–3 mm (0.059–0.118 in) wide.

Newly hatched nymphs are translucent, lighter in color, and become browner as they moult and reach maturity. A bed bug nymph of any age that has just consumed a blood meal has a bright red, translucent abdomen, fading to brown over the next several hours, and to opaque black within two days as the insect digests its meal. Bed bugs may be mistaken for other insects, such as booklice, small cockroaches, or carpet beetles; however, when warm and

active, their movements are more ant-like, and like most other true bugs, they emit a characteristic disagreeable odor when crushed.

Bed bugs use pheromones and kairomones to communicate regarding nesting locations, feeding, and reproduction.

The lifespan of bed bugs varies by species and is also dependent on feeding.

Bed bugs can survive a wide range of temperatures and atmospheric compositions.[3] Below 16 °C (61 °F), adults enter semihibernation and can survive longer; they can survive for at least five days at −10 °C (14 °F), but die after 15 minutes of exposure to −32 °C (−26 °F).[4] Common commercial and residential freezers reach temperatures low enough to kill most life stages of bed bug, with 95% mortality after 3 days at −12 °C (10 °F).[5] They show high desiccation tolerance, surviving low humidity and a 35–40 °C range even with loss of one-third of body weight; earlier life stages are more susceptible to drying out than later ones.[6]



An adult bed bug (Cimex lectularius) about 4 to 5 mm long

The thermal death point for *C. lectularius* is 45 °C (113 °F); all stages of life are killed by 7 minutes of exposure to 46 °C (115 °F).[4] Bed bugs apparently cannot survive high concentrations of carbon dioxide for very long; exposure to nearly pure nitrogen atmospheres, however, appears to have relatively little effect even after 72 hours.[7]

Household insecticides often do not have a prolonged effect on the bug population. Professional pest control experts may use potentially harmful substances such as chlorpyrifos.

Taxonomy

- *Cimex adjunctus*, bat bug found in Eastern United States
- *Cimex antennatus*, bat bug from Pacific North America[8]
- *Cimex brevis*
- *Cimex columbarius*, infesting pigeon nests[9]
- *Cimex emarginatus*, bat bug from the Balkan Peninsula[10]
- *Cimex incrassatus*,
- *Cimex japonicus*, bat bug found in Japan
- *Cimex latipennis*, bat bug from Pacific North America[8]
- *Cimex lectularius*, common bed bug with cosmopolitan distribution
- *Cimex hemipterus*, tropical bed bug[11]
- *Cimex pilosellus*, bat bug found in northern United States and Canada[12]
- *Cimex pipistrelli*, European bat bug[13]

Feeding habits

Bed bugs are obligatory hematophagous (bloodsucking) insects. Most species feed on humans only when other prey are unavailable.[14][15][16] They obtain all the additional moisture they need from water vapor in the surrounding air.[17] Bed bugs are attracted to their hosts primarily by carbon dioxide, secondarily by warmth, and also by certain chemicals.[18][19][20] Bed bugs prefer exposed skin, preferably the face, neck, and arms of a sleeping person.

Bed bugs have mouth parts that saw through the skin, and inject saliva with anticoagulants and painkillers. Sensitivity of humans varies from extreme allergic reaction to no reaction at all (about 20%). The bite usually produces a swelling with no red spot, but when many bugs feed on a small area, reddish spots may appear after the swelling subsides.[4] The bite marks may appear in a straight line.[21]



Scanning electron micrograph (SEM) digitally colorized with skin-piercing mouthparts highlighted in purple and red

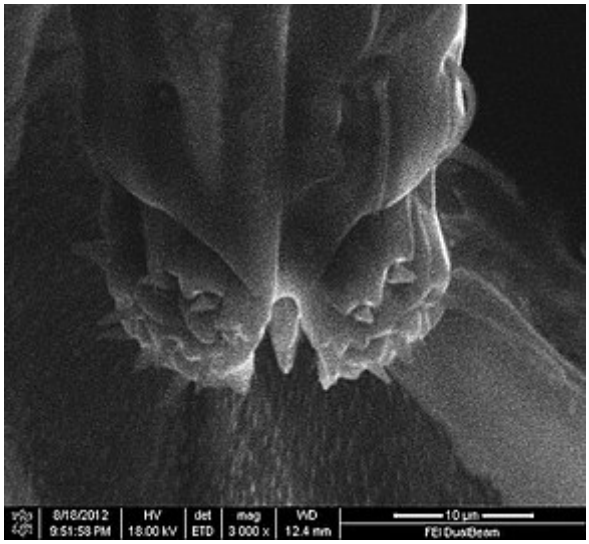
Although under certain cool conditions adult bed bugs can live for over a year without feeding,[22] under typically warm conditions they try to feed at five- to ten-day intervals, and adults can survive for about five months without food.[23] Younger instars cannot survive nearly as long, though even the vulnerable newly hatched first instars can survive for weeks without taking a blood meal.

At the 57th annual meeting of the Entomological Society of America in 2009, newer generations of pesticide-resistant bed bugs in Virginia were reported to survive only two months without feeding.[24]

DNA from human blood meals can be recovered from bed bugs for up to 90 days, which means they can be used for forensic purposes in identifying on whom the bed bugs have fed.[25][26]

Feeding physiology

A bed bug pierces the skin of its host with a stylet fascicle, rostrum, or "beak". The rostrum is composed of the maxillae and mandibles, which have been modified into elongated shapes from a basic, ancestral style. The right and left maxillary stylets are connected at their midline and a section at the centerline forms a large food canal and a smaller salivary canal. The entire maxillary and mandibular bundle penetrates the skin.[27]



Rostrum tip

The tips of the right and left maxillary stylets are not the same; the right is hook-like and curved, and the left is straight. The right and left mandibular stylets extend along the outer sides of their respective maxillary stylets and do not reach anywhere near the tip of the fused maxillary stylets. The stylets are retained in a groove in the labium, and during feeding, they are freed from the groove as the jointed labium is bent or folded out of the way; its tip never enters the wound.[27]

The mandibular stylet tips have small teeth, and through alternately moving these stylets back and forth, the insect cuts a path through tissue for the maxillary bundle to reach an appropriately sized blood vessel. Pressure from the blood vessel itself fills the insect with blood in three to five minutes. The bug then withdraws the stylet bundle from the feeding position and retracts it back into the labial groove, folds the entire unit back under the head, and returns to its hiding place.[27] It takes between five and ten minutes for a bed bug to become completely engorged with blood.[28] In all, the insect may spend less than 20 minutes in physical contact with its host, and does not try to feed again until it has either completed a moult or, if an adult, has thoroughly digested the meal.

Reproduction

North Carolina State University found that bed bugs in contrast to most other insects tolerate incest and are able to genetically withstand the effects of inbreeding quite well.[29] Male bed bugs sometimes attempt to mate with other males and pierce their abdomens.[30] This behaviour occurs because sexual attraction in bed bugs is based primarily on size, and males mount any freshly fed partner regardless of sex.[31]


Male bed bug traumatically inseminating a female

All bed bugs mate by traumatic insemination.[32][33] Female bed bugs possess a reproductive tract that functions during oviposition, but the male does not use this tract for sperm insemination.[32] Instead, the male pierces the female's abdomen with his hypodermic penis and ejaculates into the body cavity. In all bed bug species except *Primicimex cavernis*, sperm are injected into the mesospermalege,[32] a component of the spermalege,[32] a secondary genital structure that reduces the wounding and immunological costs of traumatic insemination.[34][35][36] Injected sperm travel via the haemolymph (blood) to sperm storage structures called seminal conceptacles, with fertilisation eventually taking place at the ovaries.[35]

The "bed bug alarm pheromone" consists of (*E*)-2-octenal and (*E*)-2-hexenal. It is released when a bed bug is disturbed, as during an attack by a predator. A 2009 study demonstrated the alarm pheromone is also released by male bed bugs to repel other males that attempt to mate with them.[36][37]

Cimex lectularius and *C. hemipterus* mate with each other given the opportunity, but the eggs then produced are usually sterile. In a 1988 study, one of 479 eggs was fertile and resulted in a hybrid, *Cimex hemipterus* × *lectularius*.[38][39]

Sperm protection

Cimex lectularius males have environmental microbes on their genitals. These microbes damage sperm cells, leaving them unable to fertilize female gametes. Due to these dangerous microbes, males have evolved antimicrobial ejaculate substances that prevent sperm damage. When the microbes contact sperm or the male genitals, the bed bug releases antimicrobial substances. Many species of these microbes live in the bodies of females after mating. The microbes can cause infections in the females. It has been suggested that females receive benefit from the ejaculate. Although the benefit is not direct, females are able to produce more eggs than optimum increasing the amount of the females' genes in the gene pool.[40]

Sperm and seminal fluid allocation

In organisms, sexual selection extends past differential reproduction to affect sperm composition, sperm competition, and ejaculate size. Males of *C. lectularius* allocate 12% of their sperm and 19% of their seminal fluid per mating. Due to these findings, Reinhard et. al proposed that multiple mating is limited by seminal fluid and not sperm. After measuring ejaculate volume, mating rate and estimating sperm density, Reinhardt et al. showed that mating could be limited by seminal fluid. Despite these advances, the cost difference between ejaculate-dose dependence and mating frequency dependence have not been explored.[41]

Egg production

Males fertilize females only by traumatic insemination into the structure called the ectospermalege (the organ of Berlese, however the organ of Ribaga, as it was first named, was first designated as an organ of stridulation. These two names are not descriptive, so other terminologies are used). On fertilization, the female's ovaries finish developing, which suggests that sperm plays a role

other than fertilizing the egg. Fertilization also allows for egg production through the corpus allatum. Sperm remains viable in a female's spermathecae (a better term is conceptacle), a sperm-carrying sack, for a long period of time as long as body temperature is optimum. The female lays fertilized eggs until she depletes the sperm found in her conceptacle. After the depletion of sperm, she lays a few sterile eggs. The number of eggs a *C. lectularius* female produces does not depend on the sperm she harbors, but on the female's nutritional level.[42]

Alarm pheromones

In *C. lectularius*, males sometimes mount other males because male sexual interest is directed at any recently fed individual regardless of their sex, but unfed females may also be mounted. Traumatic insemination is the only way for copulation to occur in bed bugs. Females have evolved the spermalege to protect themselves from wounding and infection. Because males lack this organ, traumatic insemination could leave them badly injured. For this reason, males have evolved alarm pheromones to signal their sex to other males. If a male *C. lectularius* mounts another male, the mounted male releases the pheromone signal and the male on top stops before insemination.

Females are capable of producing alarm pheromones to avoid multiple mating, but they generally do not do so. Two reasons are proposed as to why females do not release alarm pheromones to protect themselves. First, alarm pheromone production is costly. Due to egg production, females may refrain from spending additional energy on alarm pheromones. The second proposed reason is that releasing the alarm pheromone reduces the benefits associated with multiple mating.[43] Benefits of multiple mating include material benefits, better quality nourishment or more nourishment, genetic benefits including increased fitness of offspring, and finally, the cost of resistance may be higher than the benefit of consent—which appears the case in *C. lectularius*.[44]

Life stages

Bed bugs have five immature nymph life stages and a final sexually mature adult stage.[45] They shed their skins through ecdysis at each stage, discarding their outer exoskeleton, which is somewhat clear, empty exoskeletons of the bugs themselves. Bed bugs must molt six times before becoming fertile adults, and must consume at least one blood meal to complete each molt.[46]

Each of the immature stages lasts about a week, depending on temperature and the availability of food, and the complete lifecycle can be completed in as little as two months (rather long compared to other ectoparasites). Fertilized females with enough food lay three to four eggs each day continually until the end of their lifespans (about nine months under warm conditions), possibly generating as many as 500 eggs in this time.[46] Genetic analysis has shown that a single pregnant bed bug, possibly a single survivor of eradication, can be responsible for an entire infestation over a matter of weeks, rapidly producing generations of offspring.[47]



Slide of *C. lectularius*



On the right is recently sloughed skin from its nymph stage



Nymph feeding on host



Blood-fed stage (note differences in color with respect to digestion of blood meal)

Sexual dimorphism

Sexual dimorphism occurs in *C. lectularius*, with the females larger in size than the males on average. The abdomens of the sexes differ in that the males appear to have "pointed" abdomens, which are actually their copulatory organs, while females have more rounded abdomens. Since males are attracted to large body size, any bed bug with a recent blood meal can be seen as a potential mate. However, males will mount unfed, flat females on occasion. The female is able to curl her abdomen forward and underneath toward the head to not mate. Males are generally unable to discriminate between the sexes until after mounting, but before inseminating.[48]

Host searching

Cimex lectularius only feeds every five to seven days, which suggests that it does not spend the majority of its life searching for a host. When a bed bug is starved, it leaves its shelter and searches for a host. If it successfully feeds, it returns to its shelter; otherwise, it continues to search for a host. After searching—regardless of whether or not it has eaten—the bed bug returns to the shelter to aggregate before the photophase (period of light during a day-night cycle). Reis argues that two reasons explain why *C. lectularius* would return to its shelter and aggregate after feeding. One is to find a mate and the other is to find shelter to avoid getting smashed after eating.[49]

Aggregation and dispersal behavior

Cimex lectularius aggregates under all life stages and mating conditions. Bed bugs may choose to aggregate because of predation, resistance to desiccation, and more opportunities to find a mate. Airborne pheromones are responsible for aggregations. Another source of aggregation could be the recognition of other *C. lectularius* bugs through mechanoreceptors located on their antennae. Aggregations are formed and disbanded based on the associated cost and benefits. Females are more often found separate from the aggregation than males. Females are more likely to expand the population range and find new sites. Active female dispersal can account for treatment failures. Males, when found in areas with few females, abandon an aggregation to find a new mate. The males excrete an aggregation pheromone into the air that attracts virgin females and arrests other males.[50]

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Beetle

Beetles are a group of insects that form the order **Coleoptera**, in the superorder Endopterygota. Their front pair of wings are hardened into wing-cases, elytra, distinguishing them from most other insects. The Coleoptera, with about 400,000 species, is the largest of all orders, constituting almost 40% of described insects and 25% of all known animal life-forms; new species are discovered frequently. The largest of all families, the Curculionidae (weevils), with some 83,000 member species, belongs to this order. Found in almost every habitat except the sea and the polar regions, they interact with their ecosystems in several ways: beetles often feed on plants and fungi, break down animal and plant debris, and eat other invertebrates. Some species are serious agricultural pests, such as the Colorado potato beetle, while others such as Coccinellidae (ladybirds or ladybugs) eat aphids, scale insects, thrips, and other plant-sucking insects that damage crops.

Beetles typically have a particularly hard exoskeleton including the elytra, though some such as the rove beetles have very short elytra while blister beetles have softer elytra. The general anatomy of a beetle is quite uniform and typical of insects, although there are several examples of novelty, such as adaptations in water beetles which trap air bubbles under the elytra for use while diving. Beetles are endopterygotes, which means that they undergo complete metamorphosis, with a series of conspicuous and relatively abrupt changes in body structure between hatching and becoming adult after a relatively immobile pupal stage. Some, such as stag beetles, have a marked sexual dimorphism, the males possessing enormously enlarged mandibles which they use to fight other males. Many beetles are aposematic, with bright colours and patterns warning of their toxicity, while others are harmless Batesian mimics of such insects. Many beetles, including those that live in sandy places, have effective camouflage.

Beetles are prominent in human culture, from the sacred scarabs of ancient Egypt to beetlewing art and use as pets or fighting insects for entertainment and gambling. Many beetle groups are brightly and attractively coloured making them objects of collection and decorative displays. Over 300 species are used as food, mostly as larvae; species widely consumed include mealworms and rhinoceros beetle larvae. However, the major impact of beetles on human life is as agricultural, forestry, and horticultural pests. Serious pests include the boll weevil of cotton, the Colorado potato beetle, the coconut hispine beetle, and the mountain pine beetle. Most beetles, however, do not cause economic damage and many, such as the lady beetles and dung beetles are beneficial by helping to control insect pests.

Contents

Etymology

Distribution and diversity

Evolution

- Late Paleozoic
- Jurassic
- Cretaceous

Beetle

Temporal range: 318–0 Ma

PreЄ Є O S D C P T J K PgN

Late Carboniferous–Holocene



Clockwise from top left: female golden stag beetle (*Lamprima aurata*), rhinoceros beetle (*Megasoma* sp.), long nose weevil (*Rhinotia hemistictus*), cowboy beetle (*Chondropyga dorsalis*), and a species of *Amblytelus*.

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
(unranked):	Endopterygota
Order:	Coleoptera Linnaeus, 1758

Suborders

- Adephaga
- Archostemata
- Myxophaga
- Polyphaga
- †Protocoleoptera[1]

See subgroups of the order Coleoptera

- Cenozoic

Phylogeny

External morphology
- Head
- Thorax
- Legs
- Wings
- Abdomen

Anatomy and physiology
- Digestive system
- Nervous system
- Respiratory system
- Circulatory system
- Specialized organs

Reproduction and development
- Mating
- Life cycle
 - Egg
 - Larva
 - Pupa and adult

Behaviour
- Locomotion
- Communication
- Parental care
- Eusociality
- Feeding

Ecology
- Anti-predator adaptations
 - Camouflage
 - Mimicry and aposematism
 - Other defences
- Parasitism
- Pollination
- Mutualism
- Tolerance of extreme environments
- Migration

Relationship to humans
- In ancient cultures
- As pests
- As beneficial resources
- As food and medicine
- As biodiversity indicators
- In art and adornment
- In entertainment
- As pets
- As things to collect
- As inspiration for technologies
- In conservation

Notes

References
- Bibliography

Further reading

External links

Etymology

The name of the taxonomic order, Coleoptera, comes from the Greek *koleopteros* (κολεόπτερος), given to the group by Aristotle for their elytra, hardened shield-like forewings, from *koleos*, sheath, and *pteron*, wing. The English name beetle comes from the Old English word *bitela*, little biter, related to *bītan* (to bite),[2][3] leading to Middle English *betylle*.[4] Another Old English name for beetle is *ċeafor*, chafer, used in names such as cockchafer, from the Proto-Germanic **kebrô* ("beetle"; compare German *Käfer*, Dutch *kever*).[5]



Coleoptera at the Staatliches Museum für Naturkunde Karlsruhe, Germany

Distribution and diversity

Beetles are by far the largest order of insects: the roughly 400,000 species make up about 40% of all insect species so far described, and about 25% of all animals.[1][6][7][8][9][10] A 2015 study provided four independent estimates of the total number of beetle species, giving a mean estimate of some 1.5 million with a "surprisingly narrow range"[11] spanning all four estimates from a minimum of 0.9 to a maximum of 2.1 million beetle species. The four estimates made use of host-specificity relationships (1.5 to 1.9 million), ratios with other taxa (0.9 to 1.2 million), plant:beetle ratios (1.2 to 1.3), and extrapolations based on body size by year of description (1.7 to 2.1 million).[11][12]

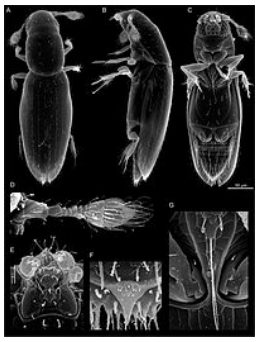
Beetles are found in nearly all habitats, including freshwater and coastal habitats, wherever vegetative foliage is found, from trees and their bark to flowers, leaves, and underground near roots - even inside plants in galls, in every plant tissue, including dead or decaying ones.[13] Tropical forest canopies have a large and diverse fauna of beetles,[14] including Carabidae,[15] Chrysomelidae,[16] and Scarabaeidae.[17]

The heaviest beetle, indeed the heaviest insect stage, is the larva of the goliath beetle, *Goliathus goliatus*, which can attain a mass of at least 115 g (4.1 oz) and a length of 11.5 cm (4.5 in). Adult male goliath beetles are the heaviest beetle in its adult stage, weighing 70–100 g (2.5–3.5 oz) and measuring up to 11 cm (4.3 in).[18] Adult elephant beetles, *Megasoma elephas* and *Megasoma actaeon* often reach 50 g (1.8 oz) and 10 cm (3.9 in).[19]

The longest beetle is the Hercules beetle *Dynastes hercules*, with a maximum overall length of at least 16.7 cm (6.6 in) including the very long pronotal horn. The smallest recorded beetle and the smallest free-living insect (as of 2015), is the featherwing beetle *Scydosella musawasensis* which may measure as little as 325 µm in length.[20]



Titan beetle, *Titanus giganteus*, a tropical longhorn, is one of the largest and heaviest insects in the world.



Scydosella musawasensis, the smallest known beetle: scale bar (right) is 50 µm.

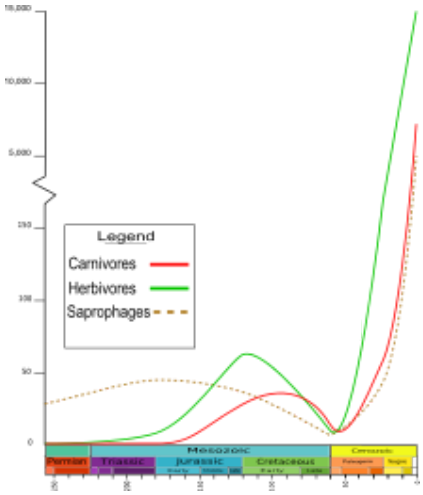


Hercules beetle, *Dynastes hercules ecuatorianus*, the longest of all beetles

Evolution

Late Paleozoic

The oldest known fossil insect that unequivocally resembles a Coleopteran is from the Lower Permian Period about 270 million years ago (mya), though these members of the family Tshekardocoleidae have 13-segmented antennae, elytra with more fully developed venation and more irregular longitudinal ribbing, and abdomen and ovipositor extending beyond the apex of the elytra. In the Permian–Triassic extinction event at the end of the Permian, some 30% of all insect species became extinct, so the fossil record of insects only includes beetles from the Lower Triassic 220 mya. Around this time, during the Late Triassic, fungus-feeding species such as Cupedidae appear in the fossil record. In the stages of the Upper Triassic, alga-feeding insects such as Triaplidae and Hydrophilidae begin to appear, alongside predatory water beetles. The first weevils, including the Obrienidae, appear alongside the first rove beetles (Staphylinidae), which closely resemble recent species.[21] Some entomologists are sceptical that such early insects are so closely related to present-day species, arguing that this is extremely unlikely; for example, the structure of the metepisternum suggests that the Obrienidae could be Archostemata, not weevils at all, despite fossils with weevil-like snouts.[22]



Beetle genera were mainly saprophages (detritivores) in the Permian and Triassic. During the Jurassic, herbivorous and then carnivorous genera became more common. In the Cenozoic, genera at all three trophic levels became far more numerous.

In 2009, a fossil beetle was described from the Pennsylvanian of Mazon Creek, Illinois, pushing the origin of the beetles to an earlier date, 318 to 299 mya.[23] Fossils from this time have been found in Asia and Europe, for instance in the red slate fossil beds of Niedermoschel near Mainz, Germany.[24] Further fossils have been found in Obora, Czech Republic and Tshekarda in the Ural mountains, Russia.[25] However, there are only a few fossils from North America before the middle Permian, although both Asia and North America had been united to Euramerica. The first discoveries from North America made in the Wellington formation of Oklahoma were published in 2005 and 2008.[21][26]

As a consequence of the Permian–Triassic extinction event, the fossil record of insects is scant, including beetles from the Lower Triassic.[27] However, there are a few exceptions, such as in Eastern Europe. At the Babiy Kamen site in the Kuznetsk Basin, numerous beetle fossils were discovered, including entire specimens of the infraorders Archostemata (e.g. Ademosynidae, Schizocoleidae), Adephaga (e.g., Triaplidae, Trachypachidae) and Polyphaga (e.g. Hydrophilidae, Byrrhidae, Elateroidea).[28] However, species from the families Cupedidae and Schizophoroidae are not present at this site, whereas they dominate at other fossil sites from the Lower Triassic such as Khey-Yaga, Russia, in the Korotaikha Basin.[21]

Jurassic

During the Jurassic (210 to 145 mya), there was a dramatic increase in the diversity of beetle families,[21] including the development and growth of carnivorous and herbivorous species. The Chrysomeloidea diversified around the same time, feeding on a wide array of plant hosts from cycads and conifers to angiosperms.[29] Close to the Upper Jurassic, the Cupedidae decreased, but the diversity of the early plant-eating species increased. Most recent plant-eating beetles feed on flowering plants or angiosperms, whose success contributed to a doubling of plant-eating species during the Middle Jurassic. However, the increase of the number of beetle families during the Cretaceous does not correlate with the increase of the number of angiosperm species.[30] Around the same time, numerous primitive weevils (e.g. Curculionoidea) and click beetles (e.g. Elateroidea) appeared. The first jewel beetles (e.g. Buprestidae) are present, but they remained rare until the Cretaceous.[31][32][33] The first scarab beetles were not coprophagous but presumably fed on rotting wood with the help of fungus; they are an early example of a mutualistic relationship.

There are more than 150 important fossil sites from the Jurassic, the majority in Eastern Europe and North Asia. Outstanding sites include Solnhofen in Upper Bavaria, Germany,[34] Karatau in South Kazakhstan,[35] the Yixian formation in Liaoning, North China,[36] as well as the Jiulongshan formation and further fossil sites in Mongolia. In North America there are only a few sites with fossil records of insects from the Jurassic, namely the shell limestone deposits in the Hartford basin, the Deerfield basin and the Newark basin.[21][37]

Cretaceous

The Cretaceous saw the fragmenting of the southern landmass, with the opening of the southern Atlantic Ocean and the isolation of New Zealand, while South America, Antarctica, and Australia grew more distant.[29] The diversity of Cupedidae and Archostemata decreased considerably. Predatory ground beetles (Carabidae) and rove beetles (Staphylinidae) began to distribute into different patterns; the Carabidae predominantly occurred in the warm regions, while the Staphylinidae and click beetles (Elateridae) preferred temperate climates. Likewise, predatory species of Cleroidea and Cucujoidea hunted their prey under the bark of trees together with the jewel beetles (Buprestidae). The diversity of jewel beetles increased rapidly, as they were the primary consumers of wood,[38] while longhorn beetles (Cerambycidae) were rather rare: their diversity increased only towards the end of the Upper Cretaceous.[21] The first coprophagous beetles are from the Upper Cretaceous[39] and may have lived on the excrement of herbivorous dinosaurs.[40] The first species where both larvae and adults are adapted to an aquatic lifestyle are found. Whirligig beetles (Gyrinidae) were moderately diverse, although other early beetles (e.g. Dytiscidae) were less, with the most widespread being the species of Coptoclavidae, which preyed on aquatic fly larvae.[21]

Many fossil sites worldwide contain beetles from the Cretaceous. Most are in Europe and Asia and belong to the temperate climate zone during the Cretaceous.[36] Lower Cretaceous sites include the Crato fossil beds in the Araripe basin in the Ceará, North Brazil, as well as overlying Santana formation; the latter was near the equator at that time. In Spain, important sites are near Montsec and Las Hoyas. In Australia, the Koonwarra fossil beds of the Korumburra group, South Gippsland, Victoria, are noteworthy. Major sites from the Upper Cretaceous include Kzyl-Dzhar in South Kazakhstan and Arkagala in Russia.[21]

Cenozoic

Beetle fossils are abundant in the Cenozoic; by the Quaternary (up to 1.6 mya), fossil species are identical to living ones, while from the Late Miocene (5.7 mya) the fossils are still so close to modern forms that they are most likely the ancestors of living species. The large oscillations in climate during the Quaternary caused beetles to change their geographic distributions so much that current location gives little clue to the biogeographical history of a species. It is evident that geographic isolation of populations must often have been broken as insects moved under the influence of changing climate, causing mixing of gene pools, rapid evolution, and extinctions, especially in middle latitudes.[42]



Fossil buprestid beetle from the Eocene (50 mya) Messel pit, which retains its structural color[41]

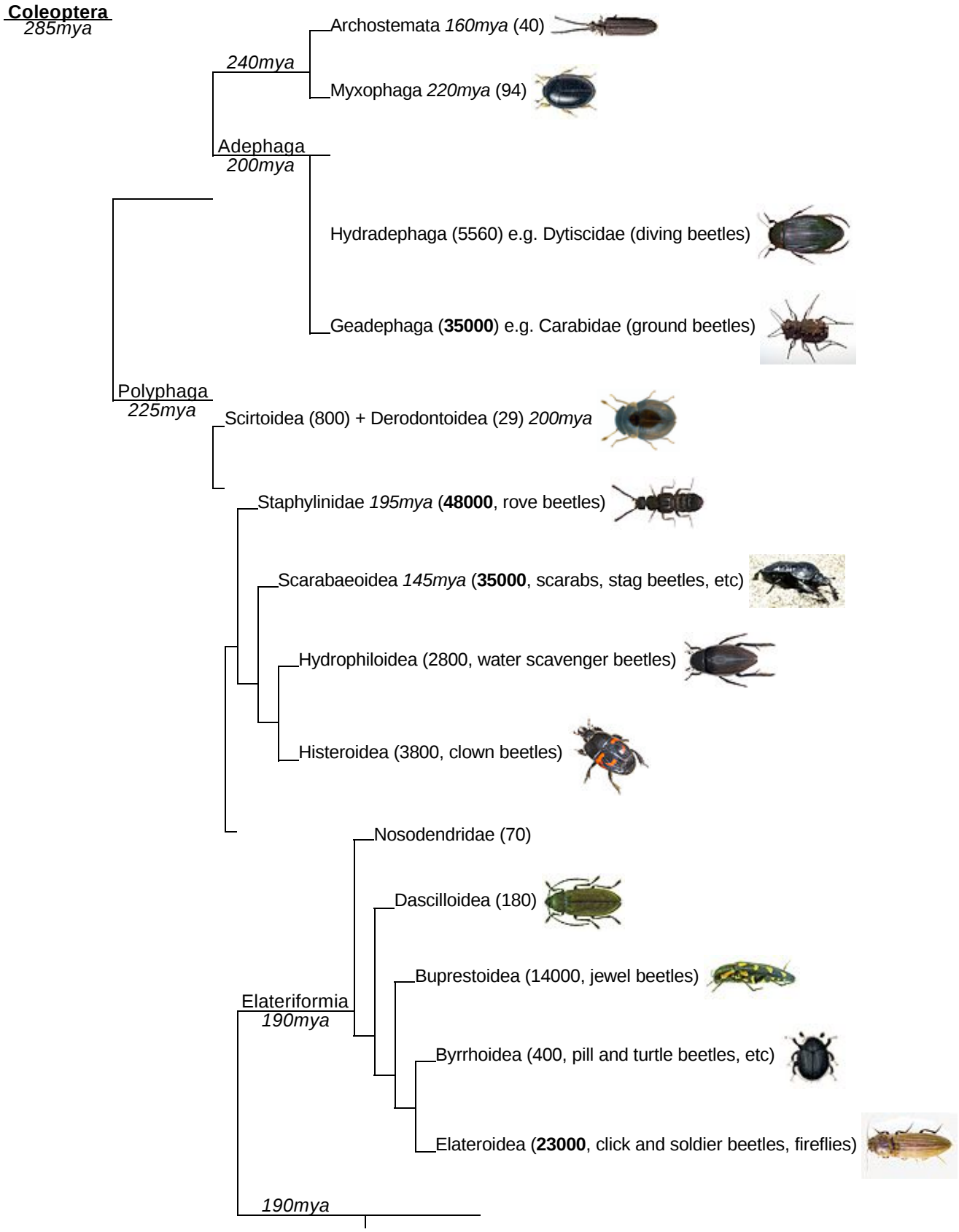
Phylogeny

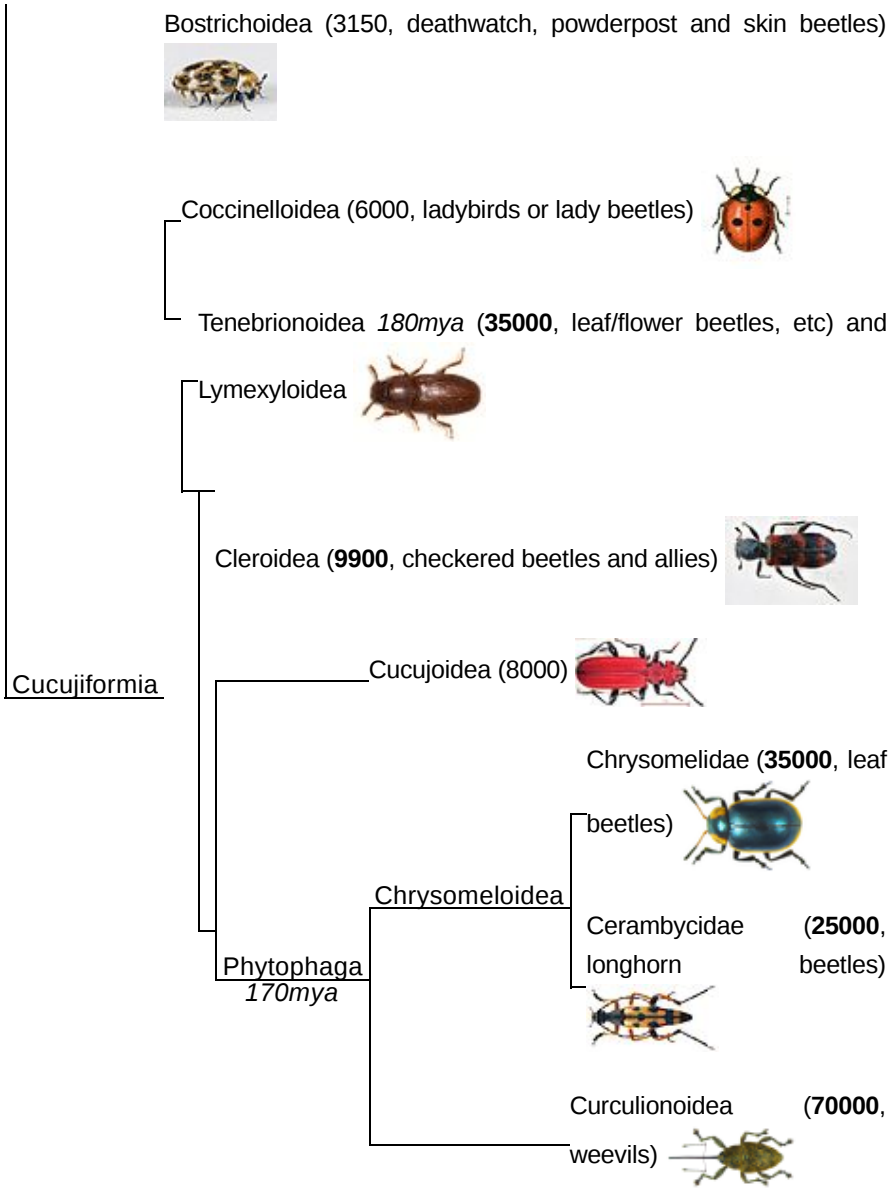
The very large number of beetle species poses special problems for classification. Some families contain tens of thousands of species, and need to be divided into subfamilies and tribes. This immense number led the evolutionary biologist J. B. S. Haldane to quip, when some theologians asked him what could be inferred about the mind of the Creator from the works of His Creation, "An inordinate fondness for beetles".[43] Polyphaga is the largest suborder, containing more than 300,000 described species in more than 170 families, including rove beetles (Staphylinidae), scarab beetles (Scarabaeidae), blister beetles (Meloidae), stag beetles (Lucanidae) and true weevils (Curculionidae).[9][44] These polyphagan beetle groups can be identified by the presence of cervical sclerites (hardened parts of the head used as points of attachment for muscles) absent in the other suborders.[45] Adephaga contains about 10 families of largely predatory beetles, includes ground beetles (Carabidae), water beetles (Dytiscidae) and whirligig beetles (Gyrinidae). In these insects, the testes are tubular and the first abdominal sternum (a plate of the exoskeleton) is divided by the hind coxae (the basal joints of the beetle's legs).[46] Archostemata contains four families of mainly wood-eating beetles, including reticulated beetles (Cupedidae) and the telephone-pole beetle.[47] The Archostemata have an exposed plate called the metatrochantin in front of the basal segment or coxa of the hind leg.[48] Myxophaga contains about 65 described species in four families, mostly very small, including Hydroscaphidae and the genus *Sphaerius*.[49] The myxophagan beetles are small and mostly alga-feeders. Their mouthparts are characteristic in lacking galeae and having a mobile tooth on their left mandible.[50]

The consistency of beetle morphology, in particular their possession of elytra, has long suggested that Coleoptera is monophyletic, though there have been doubts about the arrangement of the suborders, namely the Adephaga, Archostemata, Myxophaga and Polyphaga within that clade.[51][29][52][53][54] The twisted-wing parasites, Strepsiptera, are thought to be a sister group to the beetles, having split from them

in the Early Permian.[53][55][56][57]

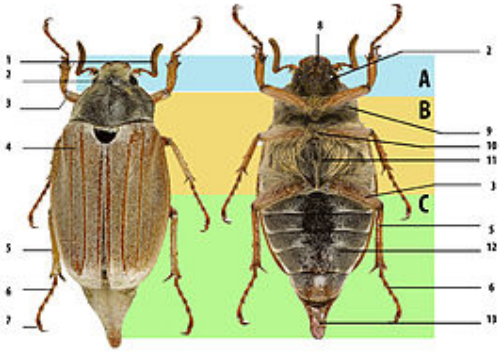
Molecular phylogenetic analysis confirms that the Coleoptera are monophyletic. Duane McKenna et al. (2015) used eight nuclear genes for 367 species from 172 of 183 Coleopteran families. They split the Adephaga into 2 clades, Hydradephaga and Geadephaga, broke up the Cucujoidea into 3 clades, and placed the Lymexyloidea within the Tenebrionoidea. The Polyphaga appear to date from the Triassic. Most extant beetle families appear to have arisen in the Cretaceous.[57] The cladogram is based on McKenna (2015).[57] The number of species in each group (mainly superfamilies) is shown in parentheses, and boldface if over 10,000.[58] English common names are given where possible. Dates of origin of major groups are shown in italics in millions of years ago (mya).[58]





External morphology

Beetles are generally characterized by a particularly hard exoskeleton and hard forewings (elytra) not usable for flying. Almost all beetles have mandibles that move in a horizontal plane. The mouthparts are rarely suctorial, though they are sometimes reduced; the maxillae always bear palps. The antennae usually have 11 or fewer segments, except in some groups like the Cerambycidae (longhorn beetles) and the Rhipiceridae (cicada parasite beetles). The coxae of the legs are usually located recessed within a coxal cavity. The genitalic structures are telescoped into the last abdominal segment in all extant beetles. Beetle larvae can often be confused with those of other endopterygote groups.[48] The beetle's exoskeleton is made up of numerous plates, called sclerites, separated by thin sutures. This design provides armored defenses while maintaining flexibility. The general anatomy of a beetle is quite uniform, although specific organs and appendages vary greatly in appearance and function between the many families in the order. Like all insects, beetles' bodies are divided into three sections: the head, the thorax, and the abdomen.[7] Because there are so many species, identification is quite difficult, and



Beetle body structure, using cockchafer. A: head, B: thorax, C: abdomen. 1: antenna, 2: compound eye, 3: femur, 4: elytron (wing cover), 5: tibia, 6: tarsus, 7: claws, 8: mouthparts, 9: prothorax, 10: mesothorax, 11: metathorax, 12: abdominal sternites, 13: pygidium.

relies on attributes including the shape of the antennae, the tarsal formulae[a] and shapes of these small segments on the legs, the mouthparts, and the ventral plates (sterna, pleura, coxae). In many species accurate identification can only be made by examination of the unique male genitalic structures.[59]

Head

The head, having mouthparts projecting forward or sometimes downturned, is usually heavily sclerotized and is sometimes very large.[6] The eyes are compound and may display remarkable adaptability, as in the case of the aquatic whirligig beetles (Gyrinidae), where they are split to allow a view both above and below the waterline. A few Longhorn beetles (Cerambycidae) and weevils as well as some fireflies (Rhagophthalmidae) [60] have divided eyes, while many have eyes that are notched, and a few have ocelli, small, simple eyes usually farther back on the head (on the vertex); these are more common in larvae than in adults.[61] The anatomical organization of the compound eyes may be modified and depends on whether a species is primarily crepuscular, or diurnally or nocturnally active.[62] Ocelli are found in the adult carpet beetle (Dermestidae), some rove beetles (Omaliinae), and the Derodontidae.[61]



Polyphylla fullo has distinctive fan-like antennae, one of several distinct forms for the appendages among beetles.

Beetle antennae are primarily organs of sensory perception and can detect motion, odour and chemical substances,[63] but may also be used to physically feel a beetle's environment. Beetle families may use antennae in different ways. For example, when moving quickly, tiger beetles may not be able to see very well and instead hold their antennae rigidly in front of them in order to avoid obstacles.[64] Certain Cerambycidae use antennae to balance, and blister beetles may use them for grasping. Some aquatic beetle species may use antennae for gathering air and passing it under the body whilst submerged. Equally, some families use antennae during mating, and a few species use them for defence. In the cerambycid *Onychocerus albitarsis*, the antennae have venom injecting structures used in defence, which is unique among arthropods.[65] Antennae vary greatly in form, sometimes between the sexes, but are often similar within any given family. Antennae may be clubbed, threadlike, angled, shaped like a string of beads, comb-like (either on one side or both, bipectinate), or toothed. The physical variation of antennae is important for the identification of many beetle groups. The Curculionidae have elbowed or geniculate antennae. Feather like flabellate antennae are a restricted form found in the Rhipiceridae and a few other families. The Silphidae have a capitate antennae with a spherical head at the tip. The Scarabaeidae typically have lamellate antennae with the terminal segments extended into long flat structures stacked together. The Carabidae typically have thread-like antennae. The antennae arises between the eye and the mandibles and in the Tenebrionidae, the antennae rise in front of a notch that breaks the usually circular outline of the compound eye. They are segmented and usually consist of 11 parts, the first part is called the scape and the second part is the pedicel. The other segments are jointly called the flagellum.[63][66][67]

Beetles have mouthparts like those of grasshoppers. The mandibles appear as large pincers on the front of some beetles. The mandibles are a pair of hard, often tooth-like structures that move horizontally to grasp, crush, or cut food or enemies (see defence, below). Two pairs of finger-like appendages, the maxillary and labial palpi, are found around the mouth in most beetles, serving to move food into the mouth. In many species, the mandibles are sexually dimorphic, with those of the males enlarged enormously compared with those of females of the same species.[6]

Thorax

The thorax is segmented into the two discernible parts, the pro- and pterothorax. The pterothorax is the fused meso- and metathorax, which are commonly separated in other insect species, although flexibly articulate from the prothorax. When viewed from below, the thorax is that part from which all three pairs of legs and both pairs of wings arise. The abdomen is everything posterior to the thorax.[7] When viewed from above, most beetles appear to have three clear sections, but this is deceptive: on the beetle's upper surface, the middle section is a hard plate called the pronotum, which is only the front part of the thorax; the back part of the thorax is concealed by the beetle's wings. This further segmentation is usually best seen on the abdomen.[68]

Legs

The multisegmented legs end in two to five small segments called tarsi. Like many other insect orders, beetles have claws, usually one pair, on the end of the last tarsal segment of each leg. While most beetles use their legs for walking, legs have been variously adapted for other uses. Aquatic beetles including the Dytiscidae (diving beetles), Haliplidae, and many species of Hydrophilidae, the legs, often the last pair, are modified for swimming, typically with rows of long hairs. Male diving beetles have suctorial cups on their forelegs that they use to grasp females.[69] Other beetles have fossorial legs widened and often spined for digging. Species with such adaptations are found among the scarabs, ground beetles, and clown beetles (Histeridae). The hind legs of some beetles, such as flea beetles (within Chrysomelidae) and flea weevils (within Curculionidae), have enlarged femurs that help them leap.[70]



Acilius sulcatus, a diving beetle with hind legs adapted as swimming limbs

Wings



Checkered beetle *Trichodes alvearius* taking off, showing the hard elytra (forewings adapted as wing-cases) held stiffly away from the flight wings

The forewings of beetles are not used for flight, but form elytra which cover the hind part of the body and protect the hindwings. The elytra are usually hard shell-like structures which must be raised to allow the hind wings to move for flight.[71] However, in the soldier beetles (Cantharidae), the elytra are soft, earning this family the name of leatherwings.[72] Other soft wing beetles include the net-winged beetle *Calopteron discrepans*, which has brittle wings that rupture easily in order to release chemicals for defence.[73]

Beetles' flight wings are crossed with veins and are folded after landing, often along these veins, and stored below the elytra. A fold (*jugum*) of the membrane at the base of each wing is characteristic.[71] Some beetles have lost the ability to fly. These include some ground beetles (Carabidae) and some true weevils (Curculionidae), as well as desert- and cave-dwelling species of other families. Many have the two elytra fused together, forming a solid shield over the abdomen. In a few families, both the ability to fly and the elytra have been lost, as in the glow-worms (Phengodidae), where the females resemble larvae throughout their lives.[74] The presence of elytra and wings does not always indicate that the beetle will fly. For example, the tansy beetle walks between habitats despite being physically capable of flight.[75]

Abdomen

The abdomen is the section behind the metathorax, made up of a series of rings, each with a hole for breathing and respiration, called a spiracle, composing three different segmented sclerites: the tergum, pleura, and the sternum. The tergum in almost all species is membranous, or usually soft and concealed by the wings and elytra when not in flight. The pleura are usually small or hidden in some species, with each pleuron having a single spiracle. The sternum is the most widely visible part of the abdomen, being a more or less sclerotized segment. The abdomen itself does not have any appendages, but some (for example, Mordellidae) have articulating sternal lobes.[76]

Anatomy and physiology

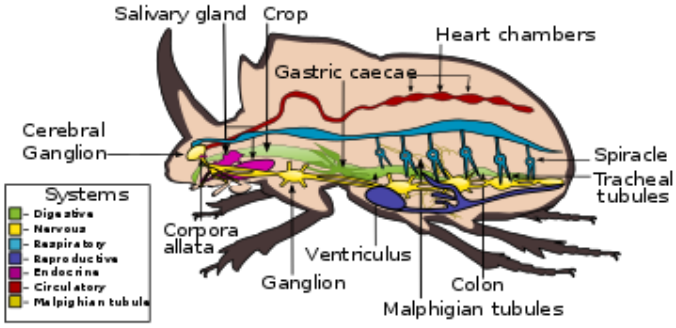
Digestive system

The digestive system of beetles is primarily adapted for a herbivorous diet. Digestion takes place mostly in the anterior midgut, although in predatory groups like the Carabidae, most digestion occurs in the crop by means of midgut enzymes. In the Elateridae, the larvae are liquid feeders that extraorally digest their food by secreting enzymes.[7] The alimentary canal basically consists of a short, narrow pharynx, a widened expansion, the crop, and a poorly developed gizzard. This is followed by the midgut, that varies in dimensions

between species, with a large amount of cecum, and the hindgut, with varying lengths. There are typically four to six Malpighian tubules.[6]

Nervous system

The nervous system in beetles contains all the types found in insects, varying between different species, from three thoracic and seven or eight abdominal ganglia which can be distinguished to that in which all the thoracic and abdominal ganglia are fused to form a composite structure.[7]



A beetle's body systems

Respiratory system


Dytiscus spiracles (right) on upper side of abdomen, normally covered by the elytra, are in contact with an air bubble when the beetle dives.

Like most insects, beetles inhale air, for the oxygen it contains, and exhale carbon dioxide, via a tracheal system. Air enters the body through spiracles, and circulates within the haemocoel in a system of tracheae and tracheoles, through whose walls the gases can diffuse.[7]

Diving beetles, such as the Dytiscidae, carry a bubble of air with them when they dive. Such a bubble may be contained under the elytra or against the body by specialized hydrophobic hairs. The bubble covers at least some of the spiracles, permitting air to enter the tracheae.[7] The function of the bubble is not only to contain a store of air but to act as a physical gill. The air that it traps is in contact with oxygenated water, so as the animal's consumption depletes the oxygen in the bubble, more oxygen can diffuse in to replenish it.[77] Carbon dioxide is more soluble in water than either oxygen or nitrogen, so it readily diffuses out faster than in. Nitrogen is the most plentiful gas in the bubble, and the least soluble, so it constitutes a relatively static component of the bubble and acts as a stable medium for respiratory gases to accumulate in and pass through. Occasional visits to the surface are sufficient for the beetle to re-establish the constitution of the bubble.[78]

Circulatory system

Like other insects, beetles have open circulatory systems, based on hemolymph rather than blood. As in other insects, a segmented tube-like heart is attached to the dorsal wall of the hemocoel. It has paired inlets or *ostia* at intervals down its length, and circulates the hemolymph from the main cavity of the haemocoel and out through the anterior cavity in the head.[79]

Specialized organs

Different glands are specialized for different pheromones to attract mates. Pheromones from species of Rutelinae are produced from epithelial cells lining the inner surface of the apical abdominal segments; amino acid-based pheromones of Melolonthinae are produced from eversible glands on the abdominal apex. Other species produce different types of pheromones. Dermestids produce esters, and species of Elateridae produce fatty acid-derived aldehydes and acetates.[7] To attract a mate, fireflies (Lampyridae) use modified fat body cells with transparent surfaces backed with reflective uric acid crystals to produce light by bioluminescence. Light production is highly efficient, by oxidation of luciferin catalyzed by enzymes (luciferases) in the presence of adenosine triphosphate (ATP) and oxygen, producing oxyluciferin, carbon dioxide, and light.[7]

Tympanal organs or hearing organs consist of a membrane (tympanum) stretched across a frame backed by an air sac and associated sensory neurons, are found in two families.[80] Several species of the genus *Cicindela* (Carabidae) have hearing organs on the dorsal surfaces of their first abdominal segments beneath the wings; two tribes in the Dynastinae (within the Scarabaeidae) have hearing organs just beneath their pronotal shields or neck membranes. Both families are sensitive to ultrasonic frequencies, with strong evidence indicating they function to detect the presence of bats by their ultrasonic echolocation.[7]

Reproduction and development

Beetles are members of the superorder Endopterygota, and accordingly most of them undergo complete metamorphosis. The typical form of metamorphosis in beetles passes through four main stages: the egg, the larva, the pupa, and the imago or adult. The larvae are commonly called grubs and the pupa sometimes is called the chrysalis. In some species, the pupa may be enclosed in a cocoon constructed by the larva towards the end of its final instar. Some beetles, such as typical members of the families Meloidae and Rhipiphoridae, go further, undergoing hypermetamorphosis in which the first instar takes the form of a triungulin.[81]

Mating



Punctate flower chafers (*Neorrhina punctata*, Scarabaeidae) mating

Some beetles have intricate mating behaviour. Pheromone communication is often important in locating a mate. Different species use different pheromones. Scarab beetles such as the Rutelinae use pheromones derived from fatty acid synthesis, while other scarabs such as the Melolonthinae use amino acids and terpenoids. Another way beetles find mates is seen in the fireflies (Lampyridae) which are bioluminescent, with abdominal light-producing organs. The males and females engage in a complex dialogue before mating; each species has a unique combination of flight patterns, duration, composition, and intensity of the light produced.[7]

Before mating, males and females may stridulate, or vibrate the objects they are on. In the Meloidae, the male climbs onto the dorsum of the female and strokes his antennae on her head, palps, and antennae. In *Eupompha*, the male draws his antennae along his longitudinal vertex. They may not mate at all if they do not perform the precopulatory ritual.[7] This mating behaviour may be different amongst dispersed populations of the same species. For example, the mating of a Russian population of tansy beetle (*Chysolina graminis*) is preceded by an elaborate ritual involving the male tapping the female's eyes, pronotum and antennae with its antennae, which is not evident in the population of this species in the United Kingdom.[82]

Competition can play a part in the mating rituals of species such as burying beetles (*Nicrophorus*), the insects fighting to determine which can mate. Many male beetles are territorial and fiercely defend their territories from intruding males. In such species, the male often has horns on the head or thorax, making its body length greater than that of a female. Copulation is generally quick, but in some cases lasts for several hours. During copulation, sperm cells are transferred to the female to fertilize the egg.[6]

Life cycle

Egg

Essentially all beetles lay eggs, though some myrmecophilous Aleocharinae and some Chrysomelinae which live in mountains or the subarctic are ovoviviparous, laying eggs which hatch almost immediately. Beetle eggs generally have smooth surfaces and are soft, though the Cupedidae have hard eggs. Eggs vary widely between species: the eggs tend to be small in species with many instars (larval stages), and in those that lay large numbers of eggs. A female may lay from several dozen to several thousand eggs during her lifetime, depending on the extent of parental care. This ranges from the simple laying of eggs under a leaf, to the parental care provided by scarab beetles, which house, feed and protect their young. The Attelabidae roll leaves and lay their eggs inside the roll for protection.[7][83]

Larva

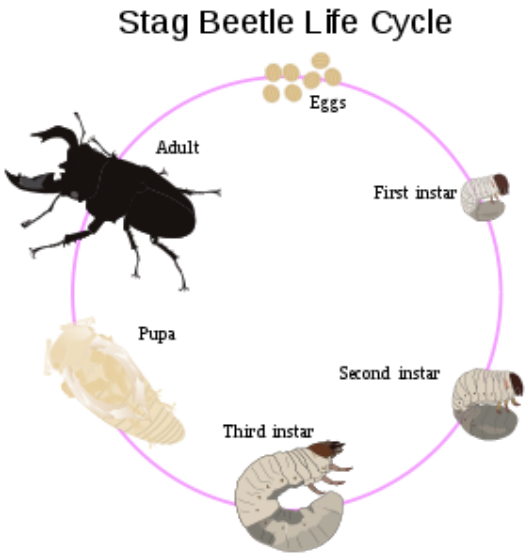
The larva is usually the principal feeding stage of the beetle life cycle. Larvae tend to feed voraciously once they emerge from their eggs. Some feed externally on plants, such as those of certain leaf beetles, while others feed within their food sources. Examples of internal feeders are most Buprestidae and longhorn beetles. The larvae of many beetle families are predatory like the adults (ground beetles, ladybirds, rove beetles). The larval period varies between species, but can be as long as several years. The larvae of skin beetles undergo a degree of reversed development when starved, and later grow back to the previously attained level of maturity. The cycle can be repeated

many times (see Biological immortality).[84] Larval morphology is highly varied amongst species, with well-developed and sclerotized heads, distinguishable thoracic and abdominal segments (usually the tenth, though sometimes the eighth or ninth).[6]



Scarabaeiform larva of Hercules beetle

Beetle larvae can be differentiated from other insect larvae by their hardened, often darkened heads, the presence of chewing mouthparts, and spiracles along the sides of their bodies. Like adult beetles, the larvae are varied in appearance, particularly between beetle families. Beetles with somewhat flattened, highly mobile larvae include the ground beetles and rove beetles; their larvae are described as campodeiform. Some beetle larvae resemble hardened worms with dark head capsules and minute legs. These are elateriform larvae, and are found in the click beetle (Elateridae) and darkling beetle (Tenebrionidae) families. Some elateriform larvae of click beetles are known as wireworms. Beetles in the Scarabaeoidea have short, thick larvae described as scarabaeiform, more commonly known as grubs.[85]



The life cycle of the stag beetle includes three instars.

All beetle larvae go through several instars, which are the developmental stages between each moult. In many species, the larvae simply increase in size with each successive instar as more food is consumed. In some cases, however, more dramatic changes occur. Among certain beetle families or genera, particularly those that exhibit parasitic lifestyles, the first instar (the planidium) is highly mobile to search out a host, while the following instars are more sedentary and remain on or within their host. This is known as hypermetamorphosis; it occurs in the Meloidae, Micromalthidae, and Ripiphoridae.[86] The blister beetle *Epicauta vittata* (Meloidae), for example, has three distinct larval stages. Its first stage, the triungulin, has longer legs to go in search of the eggs of grasshoppers. After feeding for a week it moults to the second stage, called the caraboid stage, which resembles the larva of a carabid beetle. In another week it moults and assumes the appearance of a scarabaeid larva – the scarabaeidoid stage. Its penultimate larval stage is the pseudo-pupa or the coarcate larva, which will overwinter and pupate until the next spring.[87]

The larval period can vary widely. A fungus feeding staphylinid *Phanerota fasciata* undergoes three moults in 3.2 days at room temperature while *Anisotoma* sp. (Leiodidae) completes its larval stage in the fruiting body of slime mold in 2 days and possibly represents the fastest growing beetles. Dermestid beetles, *Trogoderma inclusum* can remain in an extended larval state under unfavourable conditions, even reducing their size between moults. A larva is reported to have survived for 3.5 years in an enclosed container.[7]

Pupa and adult

As with all endopterygotes, beetle larvae pupate, and from these pupae emerge fully formed, sexually mature adult beetles, or imagos. Pupae never have mandibles (they are adecticous). In most pupae, the appendages are not attached to the body and are said to be exarate; in a few beetles (Staphylinidae, Ptiliidae etc.) the appendages are fused with the body (termed as obtect pupae).[6]

Adults have extremely variable lifespans, from weeks to years, depending on the species.[6][48] Some wood-boring beetles can have extremely long life-cycles. It is believed that when furniture or house timbers are infested by beetle larvae, the timber already contained the larvae when it was first sawn up. A birch bookcase 40 years old released adult *Eburia quadrigeminata* (Cerambycidae), while *Buprestis aurulenta* and other Buprestidae have been documented as emerging as much as 51 years after manufacture of wooden items.[88]

Behaviour

Locomotion



Photinus pyralis, firefly, in flight



The ivory-marked beetle, *Eburia quadrigeminata*, may live up to 40 years inside the hardwoods on which the larva feeds.

The elytra allow beetles to both fly and move through confined spaces, doing so by folding the delicate wings under the elytra while not flying, and folding their wings out just before takeoff. The unfolding and folding of the wings is operated by muscles attached to the wing base; as long as the tension on the radial and cubital veins remains, the wings remain straight. In some day-flying species (for example, Buprestidae, Scarabaeidae), flight does not include large amounts of lifting of the elytra, having the metathorac wings extended under the lateral elytra margins.[7] The altitude reached by beetles in flight varies. One study investigating the flight altitude of the ladybird species *Coccinella septempunctata* and *Harmonia axyridis* using radar showed that, whilst the majority in flight over a single location were at 150–195 m above ground level, some reached altitudes of over 1100 m.[89]

Many rove beetles have greatly reduced elytra, and while they are capable of flight, they most often move on the ground: their soft bodies and strong abdominal muscles make them flexible, easily able to wriggle into small cracks.[90]

Aquatic beetles use several techniques for retaining air beneath the water's surface. Diving beetles (Dytiscidae) hold air between the abdomen and the elytra when diving. Hydrophilidae have hairs on their under surface that retain a layer of air against their bodies. Adult crawling water beetles use both their elytra and their hind coxae (the basal segment of the back legs) in air retention, while whirligig beetles simply carry an air bubble down with them whenever they dive.[91]

Communication

Beetles have a variety of ways to communicate, including the use of pheromones. The mountain pine beetle emits a pheromone to attract other beetles to a tree. The mass of beetles are able to overcome the chemical defenses of the tree. After the tree's defenses have been exhausted, the beetles emit an anti-aggregation pheromone. This species can stridulate to communicate,[92] but others may use sound to defend themselves when attacked.[93]

Parental care

Parental care is found in a few families[94] of beetle, perhaps for protection against adverse conditions and predators.[7] The rove beetle *Bledius spectabilis* lives in salt marshes, so the eggs and larvae are endangered by the rising tide. The maternal beetle patrols the eggs and larvae, burrowing to keep them from flooding and asphyxiating, and protects them from the predatory carabid beetle *Dicheirotrichus gustavi* and from the parasitoidal wasp *Barycnemis blediator*, which kills some 15% of the larvae.[95]



A dung beetle rolling dung

Burying beetles are attentive parents, and participate in cooperative care and feeding of their offspring. Both parents work to bury small animal carcass to serve as a food resource for their young and build a brood chamber around it. The parents prepare the carcass and protect it from competitors and from early decomposition. After their eggs hatch, the parents keep the larvae clean of fungus and bacteria and help the larvae feed by regurgitating food for them.[96]

Some dung beetles provide parental care, collecting herbivore dung and laying eggs within that food supply, an instance of mass provisioning. Some species do not leave after this stage, but remain to safeguard their offspring.[97]

Most species of beetles do not display parental care behaviors after the eggs have been laid.[98]

Subsociality, where females guard their offspring, is well-documented in two families of Chrysomelidae, Cassidinae and Chrysomelinae.[99][100][101][102][103]

Eusociality

Eusociality involves cooperative brood care (including brood care of offspring from other individuals), overlapping generations within a colony of adults, and a division of labour into reproductive and non-reproductive groups.[104] Few organisms outside Hymenoptera exhibit this behavior; the only beetle to do so is the weevil *Austroplatypus incompertus*.[105] This Australian species lives in horizontal networks of tunnels, in the heartwood of *Eucalyptus* trees. It is one of more than 300 species of wood-boring Ambrosia beetles which distribute the spores of ambrosia fungi.[106] The fungi grow in the beetles' tunnels, providing food for the beetles and their larvae; female offspring remain in the tunnels and maintain the fungal growth, probably never reproducing.[106][105] Cooperative brood care is also found in the bess beetles (Passalidae) where the larvae feed on the semi-digested faeces of the adults.[107]

Feeding



Hycleus sp. (Meloidae) feeding on the petals of *Ipomoea carnea*

Beetles are able to exploit a wide diversity of food sources available in their many habitats. Some are omnivores, eating both plants and animals. Other beetles are highly specialized in their diet. Many species of leaf beetles, longhorn beetles, and weevils are very host-specific, feeding on only a single species of plant. Ground beetles and rove beetles (Staphylinidae), among others, are primarily carnivorous and catch and consume many other arthropods and small prey, such as earthworms and snails. While most predatory beetles are generalists, a few species have more specific prey requirements or preferences.[108]

Decaying organic matter is a primary diet for many species. This can range from dung, which is consumed by coprophagous species (such as certain scarab beetles in the Scarabaeidae), to dead animals, which are eaten by necrophagous species (such as the carrion beetles, Silphidae). Some beetles found in dung and carrion are in fact predatory. These include members of the Histeridae and Silphidae, preying on the larvae of coprophagous and necrophagous insects.[109] Many beetles feed under bark, some feed on wood while others feed on fungi growing on wood or leaf-litter. Some beetles have special mycangia, structures for the transport of fungal spores.[110]

Ecology

Anti-predator adaptations

Beetles, both adults and larvae, are the prey of many animal predators including mammals from bats to rodents, birds, lizards, amphibians, fishes, dragonflies, robberflies, reduviid bugs, ants, other beetles, and spiders.[111][112] Beetles use a variety of anti-predator adaptations to defend themselves. These include camouflage and mimicry against predators that hunt by sight, toxicity, and defensive behaviour.



A camouflaged longhorn beetle, *Ecyrus dasycerus*

Camouflage

Camouflage is common and widespread among beetle families, especially those that feed on wood or vegetation, such as leaf beetles (Chrysomelidae, which are often green) and weevils. In some species, sculpturing or various coloured scales or hairs cause beetles such as the avocado weevil *Heilipus apiatus* to resemble bird dung or other inedible objects.[111] Many beetles that live in sandy environments blend in with the coloration of that substrate.[113]

Mimicry and aposematism



Clytus arietis (Cerambycidae), a Batesian mimic of wasps

Some longhorn beetles (Cerambycidae) are effective Batesian mimics of wasps. Beetles may combine coloration with behavioural mimicry, acting like the wasps they already closely resemble. Many other beetles, including ladybirds, blister beetles, and lycid beetles secrete distasteful or toxic substances to make them unpalatable or poisonous, and are often aposematic, where bright or contrasting coloration warn off predators; many beetles and other insects mimic these chemically protected species.[114]



Blister beetles such as *Hycleus* have brilliant aposematic coloration, warning of their toxicity.

Chemical defense is important in some species, usually being advertised by bright aposematic colours. Some Tenebrionidae use their posture for releasing noxious chemicals to warn off predators. Chemical defences may serve purposes other than just protection from vertebrates, such as protection from a wide range of microbes. Some species sequester chemicals from the plants they feed on, incorporating them into their own defenses.[113]



The bloody-nosed beetle, *Timarcha tenebricosa*, defending itself by releasing a droplet of noxious red liquid (base of leg, on right)

Other species have special glands to produce deterrent chemicals. The defensive glands of carabid ground beetles produce a variety of hydrocarbons, aldehydes, phenols, quinones, esters, and acids released from an opening at the end of the abdomen. African carabid beetles (for example, *Anthia* and *Thermophilum* – *Thermophilum* is sometimes included within *Anthia*) employ the same chemicals as ants: formic acid.[114] Bombardier beetles have well-developed pygidial glands that empty from the sides of the intersegment membranes between the seventh and eighth abdominal segments. The gland is made of two containing chambers, one for hydroquinones and hydrogen peroxide, the other holding hydrogen peroxide and catalase enzymes. These chemicals mix and result in an explosive ejection, reaching a temperature of around 100 °C (212 °F), with the breakdown of hydroquinone to hydrogen, oxygen, and quinone. The oxygen propels the noxious chemical spray as a jet that can be aimed accurately at predators.[7]

Other defences

Large ground-dwelling beetles such as Carabidae, the rhinoceros beetle and the longhorn beetles defend themselves using strong mandibles, or heavily sclerotised (armored) spines or horns to deter or fight off predators.[113] Many species of weevil that feed out in the open on leaves of plants react to attack by employing a drop-off reflex. Some combine it with thanatosis, in which they close up their appendages and "play dead".[115] The click beetles (Elateridae) can suddenly catapult themselves out of danger by releasing the energy stored by a click mechanism, which consists of a stout spine on the prosternum and a matching groove in the mesosternum.[111] Some species startle an attacker by producing sounds through a process known as stridulation.[93]

Parasitism

A few species of beetles are ectoparasitic on mammals. One such species, *Platypsyllus castoris*, parasitises beavers (*Castor* spp.). This beetle lives as a parasite both as a larva and as an adult, feeding on epidermal tissue and possibly on skin secretions and wound exudates. They are strikingly flattened dorsoventrally, no doubt as an adaptation for slipping between the beavers' hairs. They are wingless and eyeless, as are many other ectoparasites.[116] Others are kleptoparasites of other invertebrates, such as the small hive beetle (*Aethina tumida*) that infests honey bee nests,[117] while many species are parasitic inquilines or commensal in the nests of ants.[118] A few groups of beetles are primary parasitoids of other insects, feeding off of, and eventually killing their hosts.[119]

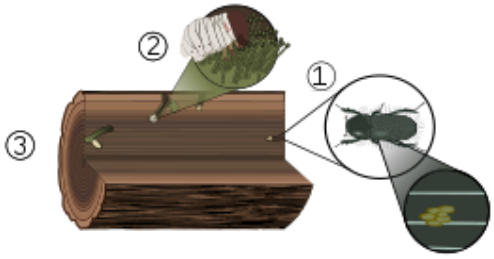
Pollination

Beetle-pollinated flowers are usually large, greenish or off-white in color, and heavily scented. Scents may be spicy, fruity, or similar to decaying organic material. Beetles were most likely the first insects to pollinate flowers. Most beetle-pollinated flowers are flattened or dish-shaped, with pollen easily accessible, although they may include traps to keep the beetle longer. The plants' ovaries are usually well protected from the biting mouthparts of their pollinators. The beetle families that habitually pollinate flowers are the Buprestidae, Cantharidae, Cerambycidae, Cleridae, Dermestidae, Lycidae, Melyridae, Mordellidae, Nitidulidae and Scarabaeidae.[120] Beetles may be particularly important in some parts of the world such as semiarid areas of southern Africa and southern California[121] and the montane grasslands of KwaZulu-Natal in South Africa.[122]



An Israeli Copper Flower-Chafer (*Protaetia cuprea ignicollis*) pollinating a crown daisy (*Glebionis coronaria*)

Mutualism



1: Adult ambrosia beetle burrows into wood and lays eggs, carrying fungal spores in its mycangia.
2: Larva feeds on fungus, which digests wood, removing toxins, to mutual benefit.
3: Larva pupates.

Mutualism is well known in a few beetles, such as the ambrosia beetle, which partners with fungi to digest the wood of dead trees. The beetles excavate tunnels in dead trees in which they cultivate fungal gardens, their sole source of nutrition. After landing on a suitable tree, an ambrosia beetle excavates a tunnel in which it releases spores of its fungal symbiont. The fungus penetrates the plant's xylem tissue, digests it, and concentrates the nutrients on and near the surface of the beetle gallery, so the weevils and the fungus both benefit. The beetles cannot eat the wood due to toxins, and uses its relationship with fungi to help overcome the defenses of its host tree in order to provide nutrition for their larvae.[123] Chemically mediated by a bacterially produced polyunsaturated peroxide,[124] this mutualistic relationship between the beetle and the fungus is coevolved.[123][125]

Tolerance of extreme environments



Beetle found in Thar Desert

About 90% of beetle species enter a period of adult diapause, a quiet phase with reduced metabolism to tide unfavourable environmental conditions. Adult diapause is the most common form of diapause in Coleoptera. To endure the period without food (often lasting many months) adults prepare by accumulating reserves of lipids, glycogen, proteins and other substances needed for resistance to future hazardous changes of environmental conditions. This diapause is induced by signals heralding the arrival of the unfavourable season; usually the cue is photoperiodic. Short (decreasing) day length serves as a signal of approaching winter and induces winter diapause (hibernation).[126] A study of hibernation in the Arctic beetle *Pterostichus brevicorni* showed that the body fat levels of adults were highest in autumn with the alimentary canal filled with food, but empty by the end of January. This loss of body fat was a gradual process, occurring in combination with dehydration.[127]

All insects are poikilothermic,[128] so the ability of a few beetles to live in extreme environments depends on their resilience to unusually high or low temperatures. The bark beetle *Pityogenes chalcographus* can survive −39 °C whilst overwintering beneath tree bark;[129] the Alaskan beetle *Cucujus clavipes puniceus* is able to withstand −58 °C; its larvae may survive −100 °C.[130] At these low temperatures, the formation of ice crystals in internal fluids is the biggest threat to survival to beetles, but this is prevented through the production of antifreeze proteins that stop water molecules from grouping together. The low temperatures experienced by *Cucujus clavipes* can be survived through their deliberate dehydration in conjunction with the antifreeze proteins. This concentrates the antifreezes several fold.[131] The hemolymph of the mealworm beetle *Tenebrio molitor* contains several antifreeze proteins.[132] The Alaskan beetle *Upis ceramboides* can survive −60 °C: its cryoprotectants are xylomannan, a molecule consisting of a sugar bound to a fatty acid,[133] and the sugar-alcohol, threitol.[134]

Conversely, desert dwelling beetles are adapted to tolerate high temperatures. For example, the Tenebrionid beetle *Onymacris rugatipennis* can withstand 50 °C.[135] Tiger beetles in hot, sandy areas are often whitish (for example, *Habroscelimorpha dorsalis*), to reflect more heat than a darker colour would. These beetles also exhibits behavioural adaptions to tolerate the heat: they are able to stand erect on their tarsi to hold their bodies away from the hot ground, seek shade, and turn to face the sun so that only the front parts of their heads are directly exposed.[136]



The fogstand beetle of the Namib Desert, *Stenocara gracilipes* is able to survive by collecting water from fog on its back.

The fogstand beetle of the Namib Desert, *Stenocara gracilipes*, is able to collect water from fog, as its elytra have a textured surface combining hydrophilic (water-loving) bumps and waxy, hydrophobic troughs. The beetle faces the early morning breeze, holding up its abdomen; droplets condense on the elytra and run along ridges towards their mouthparts. Similar adaptations are found in several other Namib desert beetles such as *Onymacris unguicularis*.[137]

Some terrestrial beetles that exploit shoreline and floodplain habitats have physiological adaptations for surviving floods. In the event of flooding, adult beetles may be mobile enough to move away from flooding, but larvae and pupa often cannot. Adults of *Cicindela togata* are unable to survive immersion in water, but larvae are able to survive a prolonged period, up to 6 days, of anoxia during floods. Anoxia tolerance in the larvae may have been sustained by switching to anaerobic metabolic pathways or by reducing metabolic rate.[138] Anoxia tolerance in the adult Carabid beetle *Pelophilia borealis* was tested in laboratory conditions and it was found that they could survive a continuous period of up to 127 days in an atmosphere of 99.9% nitrogen at 0 °C.[139]

Migration

Many beetle species undertake annual mass movements which are termed as migrations. These include the pollen beetle *Meligethes aeneus*[140] and many species of coccinellids.[141] These mass movements may also be opportunistic, in search of food, rather than seasonal. A 2008 study of an unusually large outbreak of Mountain Pine Beetle (*Dendroctonus ponderosae*) in British Columbia found that beetles were capable of flying 30–110 km per day in densities of up to 18, 600 beetles per hectare.[142]

Relationship to humans

In ancient cultures

ḫpr
in hieroglyphs

Several species of dung beetle, especially the sacred scarab, *Scarabaeus sacer*, were revered in Ancient Egypt.[143][144] The hieroglyphic image of the beetle may have had existential, fictional, or ontologic significance.[145] Images of the scarab in bone, ivory, stone, Egyptian faience, and precious metals are known from the Sixth Dynasty and up to the period of Roman rule. The scarab was of prime significance in the funerary cult of ancient Egypt.[146] The scarab was linked to Khepri, the god of the rising sun, from the supposed resemblance of the rolling of the dung ball by the beetle to the rolling of the sun by the god.[143] Some of ancient Egypt's neighbors adopted the scarab motif for seals of varying types. The best-known of these are the Judean LMLK seals, where eight of 21 designs contained scarab beetles, which were used exclusively to stamp impressions on storage jars during the reign of Hezekiah.[147] Beetles are mentioned as a symbol of the sun, as in ancient Egypt, in Plutarch's 1st century *Moralia*.[148] The Greek Magical Papyri of the 2nd century BC to the 5th century AD describe scarabs as an ingredient in a spell.[149]



A scarab in the Valley of the Kings

Pliny the Elder discusses beetles in his *Natural History*,[150] describing the stag beetle: "Some insects, for the preservation of their wings, are covered with a erust (elytra) – the beetle, for instance, the wing of which is peculiarly fine and frail. To these insects a sting has been denied by Nature; but in one large kind we find horns of a remarkable length, two-pronged at the extremities, and forming pincers, which the animal closes when it is its intention to bite."[151][152] The stag beetle is recorded in a Greek myth by Nicander and recalled by Antoninus Liberalis in which Cerambus[b] is turned into a beetle: "He can be seen on trunks and has hook-teeth, ever moving his jaws together. He is black, long and has hard wings like a great dung beetle".[153] The story concludes with the comment that the beetles were used as toys by young boys, and that the head was removed and worn as a pendant.[152][154]

As pests



Cotton boll weevil

About 75% of beetle species are phytophagous in both the larval and adult stages. Many feed on economically important plants and stored plant products, including trees, cereals, tobacco, and dried fruits.[6] Some, such as the boll weevil, which feeds on cotton buds and flowers, can cause extremely serious damage to agriculture. The boll weevil crossed the Rio Grande near Brownsville, Texas, to enter the United States from Mexico around 1892,[155] and had reached southeastern Alabama by 1915. By the mid-1920s, it had entered all cotton-growing regions in the US, traveling 40 to 160 miles (60–260 km) per year. It remains the most destructive cotton pest in North America. Mississippi State University has estimated, since the boll weevil entered the United States, it has cost cotton producers about $13 billion, and in recent times about $300 million per year.[155]

The bark beetle, elm leaf beetle and the Asian longhorned beetle (*Anoplophora glabripennis*)[156] are among the species that attack elm trees. Bark beetles (Scolytidae) carry Dutch elm disease as they move from infected breeding sites to healthy trees. The disease has devastated elm trees across Europe and North America.[157]

Some species of beetle have evolved immunity to insecticides. For example, the Colorado potato beetle, *Leptinotarsa decemlineata*, is a destructive pest of potato plants. Its hosts include other members of the Solanaceae, such as nightshade, tomato, eggplant and capsicum, as well as the potato. Different populations have between them developed resistance to all major classes of insecticide.[158] The Colorado potato beetle was evaluated as a tool of entomological warfare during World War II, the idea being to use the beetle and its larvae to damage the crops of enemy nations.[159] Germany tested its Colorado potato beetle weaponisation program south of Frankfurt, releasing 54,000 beetles.[160]



Larvae of the Colorado potato beetle, *Leptinotarsa decemlineata*, a serious crop pest

The death watch beetle, *Xestobium rufovillosum* (Ptinidae), is a serious pest of older wooden buildings in Europe. It attacks hardwoods such as oak and chestnut, always where some fungal decay has taken or is taking place. The actual introduction of the pest into buildings is thought to take place at the time of construction.[161]

Other pests include the coconut hispine beetle, *Brontispa longissima*, which feeds on young leaves, seedlings and mature coconut trees, causing serious economic damage in the Philippines.[162] The mountain pine beetle is a destructive pest of mature or weakened lodgepole pine, sometimes affecting large areas of Canada.[163]

As beneficial resources

Beetles can be beneficial to human economics by controlling the populations of pests. The larvae and adults of some species of lady beetles (Coccinellidae) feed on aphids that are pests. Other lady beetles feed on scale insects, whitefly and mealybugs.[164] If normal food sources are scarce, they may feed on small caterpillars, young plant bugs, or honeydew and nectar.[165] Ground beetles (Carabidae) are common predators of many insect pests, including fly eggs, caterpillars, and wireworms.[166] Ground beetles can help to control weeds by eating their seeds in the soil, reducing the need for herbicides to protect crops.[167] The effectiveness of some species in reducing certain



Coccinella septempunctata, a predatory beetle beneficial to agriculture

plant populations has resulted in the deliberate introduction of beetles in order to control weeds. For example, the genus *Zygogramma* is native to North America but has been used to control *Parthenium hysterophorus* in India and *Ambrosia artemisiifolia* in Russia.[168][169]

Dung beetles (Scarabidae) have been successfully used to reduce the populations of pestilent flies, such as *Musca vetustissima* and *Haematobia exigua* which are serious pests of cattle in Australia.[170] The beetles make the dung unavailable to breeding pests by quickly rolling and burying it in the soil, with the added effect of improving soil fertility, tilth, and nutrient cycling.[171] The Australian Dung Beetle Project (1965–1985), introduced species of dung beetle to Australia from South Africa and Europe to reduce populations of *Musca vetustissima*, following successful trials of this technique in Hawaii.[170] The American Institute of Biological Sciences reports that dung beetles save the United States cattle industry an estimated US$380 million annually through burying above-ground livestock feces.[172]

The Dermestidae are often used in taxidermy and in the preparation of scientific specimens, to clean soft tissue from bones.[173] Larvae feed on and remove cartilage along with other soft tissue.[174][175]

As food and medicine

Beetles are the most widely eaten insects, with about 344 species used as food, usually at the larval stage.[176] The mealworm (the larva of the darkling beetle) and the rhinoceros beetle are among the species commonly eaten.[177] A wide range of species is also used in folk medicine to treat those suffering from a variety of disorders and illnesses, though this is done without clinical studies supporting the efficacy of such treatments.[178]



Mealworms in a bowl for human consumption

As biodiversity indicators

Due to their habitat specificity, many species of beetles have been suggested as suitable as indicators, their presence, numbers, or absence providing a measure of habitat quality. Predatory beetles such as the tiger beetles (Cicindelidae) have found scientific use as an indicator taxon for measuring regional patterns of biodiversity. They are suitable for this as their taxonomy is stable; their life history is well described; they are large and simple to observe when visiting a site; they occur around the world in many habitats, with species specialised to particular habitats; and their occurrence by species accurately indicates other species, both vertebrate and invertebrate.[179] According to the habitats, many other groups such as the rove beetles in human-modified habitats, dung beetles in savannas[180] and saproxylic beetles in forests[181] have been suggested as potential indicator species.[182]

In art and adornment

Many beetles have beautiful and durable elytra that have been used as material in arts, with beetlewing the best example.[183] Sometimes, they are incorporated into ritual objects for their religious significance. Whole beetles, either as-is or encased in clear plastic, are made into objects ranging from cheap souvenirs such as key chains to expensive fine-art jewellery. In parts of Mexico, beetles of the genus *Zopherus* are made into living brooches by attaching costume jewelry and golden chains, which is made possible by the incredibly hard elytra and sedentary habits of the genus.[184]



Zopheridae in jewellery at the Texas A&M University Insect Collection

In entertainment



Pendant watch in shape of beetle, Switzerland 1850-1900 gold, diamond, enamel

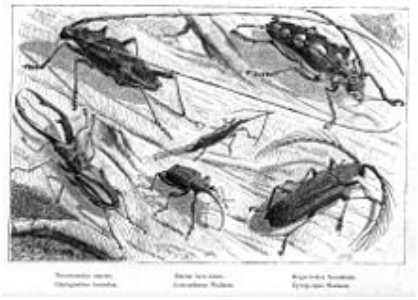
Fighting beetles are used for entertainment and gambling. This sport exploits the territorial behavior and mating competition of certain species of large beetles. In the Chiang Mai district of northern Thailand, male *Xylotrupes* rhinoceros beetles are caught in the wild and trained for fighting. Females are held inside a log to stimulate the fighting males with their pheromones.[185] These fights may be competitive and involve gambling both money and property.[186] In South Korea the Dytiscidae species *Cybister tripunctatus* is used in a roulette-like game.[187]

Beetles are sometimes used as instruments: the Onabasulu of Papua New Guinea historically used the weevil *Rhynchophorus ferrugineus* as a musical instrument by letting the human mouth serve as a variable resonance chamber for the wing vibrations of the live adult beetle.[186]

As pets

Some species of beetle are kept as pets, for example diving beetles (Dytiscidae) may be kept in a domestic fresh water tank.[188]

In Japan the practice of keeping horned rhinoceros beetles (Dynastinae) and stag beetles (Lucanidae) is particularly popular amongst young boys.[189] Such is the popularity in Japan that vending machines dispensing live beetles were developed in 1999, each holding up to 100 stag beetles.[190][191]



"Remarkable Beetles Found at Simunjon, Borneo".[c] A few of the 2000 species of beetle collected by Alfred Russel Wallace in Borneo

As things to collect

Beetle collecting became extremely popular in the Victorian era.[192] The naturalist Alfred Russel Wallace collected (by his own count) a total of 83,200 beetles during the eight years described in his 1869 book *The Malay Archipelago*, including 2,000 species new to science.[193]

As inspiration for technologies

Several coleopteran adaptations have attracted interest in biomimetics with possible commercial applications. The bombardier beetle's powerful repellent spray has inspired the development of a fine mist spray technology, claimed to have a low carbon impact compared to aerosol sprays.[194] Moisture harvesting behavior by the Namib desert beetle (*Stenocara gracilipes*) has inspired a self-filling water bottle which utilises hydrophilic and hydrophobic materials to benefit people living in dry regions with no regular rainfall.[195]

Living beetles have been used as cyborgs. A Defense Advanced Research Projects Agency funded project implanted electrodes into *Mecynorhina torquata* beetles, allowing them to be remotely controlled via a radio receiver held on its back, as proof-of-concept for surveillance work.[196] Similar technology has been applied to enable a human operator to control the free-flight steering and walking gaits of *Mecynorhina torquata* as well as graded turning and backward walking of *Zophobas morio*.[197][198][199]

In conservation

Since beetles form such a large part of the world's biodiversity, their conservation is important, and equally, loss of habitat and biodiversity is essentially certain to impact on beetles. Many species of beetles have very specific habitats and long life cycles that make them vulnerable. Some species are highly threatened while others are already feared extinct.[200] Island species tend to be more susceptible as in the case of *Helictopleurus undatus* of Madagascar which is thought to have gone extinct during the late 20th century.[201] Conservationists have attempted to arouse a liking for beetles with flagship species like the stag beetle, *Lucanus cervus*,[202] and tiger beetles (Cicindelidae). In Japan the Genji firefly, *Luciola cruciata*, is extremely popular, and in South Africa the Addo elephant dung beetle offers promise for broadening ecotourism beyond the big five tourist mammal species. Popular dislike of pest beetles, too, can be turned into public interest in insects, as can unusual ecological adaptations of species like the fairy shrimp hunting beetle, *Cicinis bruchi*.[203]

Notes

a. These count fore, mid, and hind leg tarsal segments, such as 5-5-4.

b. The wood-gnawing longhorn beetle genus *Cerambyx* is named for him.

c. The plate was labelled "Neocerambyx æneas, Cladognathus tarandus, Diurus furcellatus, Ectatorhinus Wallacei, Megacriodes Saundersii, Cyriopalpus Wallacei".

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External links

- Coleoptera (http://tolweb.org/Coleoptera/8221) from the Tree of Life Web Project
- (in German) *Käfer der Welt* (http://www.kaefer-der-welt.de/index.htm)
- Coleoptera Atlas (http://www.coleoptera-atlas.com/)
- Beetles – Coleoptera (http://www.insectlifeforms.com/Orders736/BEETLES_COLEOPTERA_60502060_736.aspx)

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Woodworm

Woodworm is the wood-eating larvae of many species of beetle. It is also a generic description given to the infestation of a wooden item (normally part of a dwelling or the furniture in it) by these larvae.[1]



The common furniture beetle (*Anobium punctatum*) *in situ*

Contents

Types of woodworm
Manifestation
Treatment
Consumption
See also
References

Types of woodworm

Woodboring beetles with larvae commonly known as woodworm include:[2][3]

- Ambrosia beetles (weevils of the subfamilies Scolytinae and Platypodinae)
- Woodboring weevils (*Pentarthrum huttoni* and *Euophryum confine*)
- Bark borer beetle (*Ernobius mollis*)
- Common furniture beetle (*Anobium punctatum*)
- Deathwatch beetle (*Xestobium rufovillosum*)
- House longhorn beetle (*Hylotrupes bajulus*)
- Powderpost beetle (*Lyctus brunneus*)
- Wharf borer (*Narcerdes melanura*)

Manifestation

Signs of woodworm usually consist of holes in the wooden item, with live infestations showing powder (faeces), known as frass, around the holes. The size of the holes varies, but are typically 1mm to 1.5mm in diameter for the most common household species, although they can be much larger in the case of House Longhorn beetle. Adult beetles which emerged from the wood may also be found in the summer months.



Wood affected by woodworm

Typically the adult beetles lay eggs on, or just under the surface of, a wooden item. The resulting grubs then feed on the wooden item causing both structural and cosmetic damage, before pupating and hatching as beetles which then breed, lay eggs, and repeat the process causing further damage.

As the beetles evolved consuming dead wood in various forest habitats, most grubs, if not all, typically require that the wooden item contain a higher moisture content than is normally found in wooden items in a typical home.

A building with a woodworm problem in the structure or furniture may well also have a problem with excess damp. The issue could be lack of ventilation in a roof space, cellar or other enclosed space within an otherwise dry building.

Whilst damp is a leading factor resulting in woodworm some species of woodboring insect, such as the Woodboring weevil, are only found in instances where fungal rot has already begun to occur.[4]

Treatment

Depending on the species involved, woodworm infestation is generally controlled with insecticides. However, some species such as the Waney Edge Borer require no treatment at all. Only active infestations require treatment, so it is important to ascertain whether an infestation is still active before treatment is carried out.[3] It is also advisable to investigate and solve possible damp issues, as dry wood is not usually affected, and wood that remains damp may be re-infected at a later date.

"Electrical insect killers", which attract and kill the adult beetles before they can breed, may be used alongside conventional chemical treatments with the intention of killing the adult beetles before they can breed, but the effectiveness of such an approach is not known.

Additionally, there are freezing treatments, which are quite effective, but take two to three weeks, and which can cause a certain amount of damage. They are quite costly. Low-oxygen treatment is effective, but very time consuming, up to eight weeks, and is often expensive.

Consumption

In some places (e.g. Cambodia, south Africa, the Philippines[5] and Papua New Guinea) people find woodworm local delicacies.

See also

- Ptinidae
- Bookworm (insect)
- List of common household pests
- Shipworm
- Woodboring beetle

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Ambrosia beetle

Ambrosia beetles are beetles of the weevil subfamilies Scolytinae and Platypodinae (Coleoptera, Curculionidae), which live in nutritional symbiosis with ambrosia fungi. The beetles excavate tunnels in dead or stressed trees in which they cultivate fungal gardens, their sole source of nutrition. After landing on a suitable tree, an ambrosia beetle excavates a tunnel in which it releases spores of its fungal symbiont. The fungus penetrates the plant's xylem tissue, extracts nutrients from it, and concentrates the nutrients on and near the surface of the beetle gallery. Ambrosia fungi are typically poor wood degraders, and instead utilize less demanding nutrients.[1] The majority of ambrosia beetles colonize xylem (sapwood and/or heartwood) of recently dead trees, but some attack stressed trees that are still alive, and a few species attack healthy trees.[2] Species differ in their preference for different parts of trees, different stages of deterioration, and in the shape of their tunnels ("galleries"). However, the majority of ambrosia beetles are not specialized to any taxonomic group of hosts, unlike most phytophagous organisms including the closely related bark beetles. One species of ambrosia beetle, *Austroplatypus incompertus* exhibits eusociality, one of the few organisms outside of Hymenoptera and Isoptera to do so.

Contents

Classification and diversity
The symbiotic relationship
Evolutionary origin
Impact on forests
See also
References
External links
Bibliography

Classification and diversity



Gallery of *Xylosandrus crassiusculus* split open, with pupae and black fungus

Until recently ambrosia beetles have been placed in independent families Scolytidae and Platypodidae, however, they are in fact some of the most highly derived weevils, and are now placed in the subfamilies Scolytinae and Platypodinae of Family Curculionidae[3] There are about 3,000 known beetle species employing the ambrosia strategy.[4]

Ambrosia beetles are an ecological guild, but not a phylogenetic clade. The ambrosia habit is an example of convergent evolution, as several groups evolved the same symbiotic relationship independently.[5] The highest diversity of ambrosia beetles is in the tropics. In the Paleotropical region, hundreds of species of Xyleborini and Platypodinae are the main agent initiating dead wood decomposition. In the Neotropics, Platypodinae and Xyleborini are joined by the scolytine tribe Cortylini. Compared to the diversity in the tropics, ambrosia beetle fauna in the temperate zone is rather limited. In the Nearctic region it is dominated by a few species from Cortylini, Xyleborini and Xyloterini. In the Palearctic ecozone, significant groups are Xyloterini and Xyleborini, joined by Scolytoplatypodini in the Far East.

The symbiotic relationship



Dinoplatypus chevrolati from Papua New Guinea, an example of Platypodinae, another species-rich group of ambrosia beetles

Beetles and their larvae graze on mycelium exposed on the gallery walls and on bodies called sporodochia, clusters of the fungus' spores. Most ambrosia beetle species don't ingest the wood tissue; instead, the sawdust resulting from the excavation is pushed out of the gallery. Following the larval and pupal stage, adult ambrosia beetles collect masses of fungal spores into their mycangia and leave the gallery to find their own tree.

A few dozen species of ambrosia fungi have been described, currently in the genera *Ambrosiella*, *Meredithiella*, and *Phialophoropsis* (from Microascales), *Afroraffaelea* and *Raffaelea* (from Ophiostomatales), *Ambrosiozyma* (Saccharomycetales), *Fusarium* and *Geosmithia* (from Hypocreales), and *Flavodon* (from Basidiomycota).[2] Many more species remain to be discovered. Little is known about the bionomy or specificity of ambrosia fungi. Ambrosia fungi are thought to be dependent on transport and inoculation provided by their beetle symbionts, as they have not been found in any other habitat. All ambrosia fungi are probably asexual and clonal.[6] Some beetles are known to acquire ("steal") fungal inoculum from fungal gardens of other ambrosia beetle species.[7]

Evolutionary origin

During their evolution, most scolytid and platypodid weevils became progressively more or less dependent on fungi regularly co-habiting dead trees. This evolution had various outcomes in different groups:

- Some phloem-eating bark beetles (phloeophages) are vectors of phytopathogenic fungi, which in some cases contribute to tree death.[8] The extent to which fungal pathogenicity benefits the beetles themselves is not at all trivial and remains disputed.[9]
- Many of phloem-feeding bark beetles use phloem-infesting fungi as an addition to their diet. Some phloeophages became dependent on such a mixed diet and evolved mycangia to transport their symbionts from maternal trees to newly infested trees.[10] These beetles are called *mycophloeophages*.
- Ambrosia beetles and ambrosia fungi are thus only one end of the spectrum of the weevil-fungus association, where both the beetle and the fungus became completely dependent on each other.[11]

Impact on forests

The vast majority of ambrosia beetles colonize dead trees, and have minor or no economic effect. A few species are able to colonize living stressed trees (Xylosandrus).[12] A few species are able to attack live and healthy trees, and those can reach epidemic proportions in non-native, invaded regions (*Xyleborus glabratus*, *Euwallacea fornicatus*[13]).

Beetle species that readily colonize lumber, such as sawlogs, green lumber, and stave-bolts, often cause region-specific economic loss from the pinhole and stained-wood defects caused by their brood galleries. In Northern USA and Canada, conifer logs are attractive to *Trypodendron lineatum* (Oliv.) during the spring swarming flight (Dyer 1967).[14] Previous studies showed that short log sections become attractive more rapidly than corresponding long logs.

See also

- Laurel wilt disease
- Forest pathology
- *Euwallacea fornicatus*
- *Xyleborus glabratus*

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External links

- Images and information (http://www.ambrosiasymbiosis.org) on the Ambrosia Symbiosis at the University of Florida.
- The MSU HISL database (https://web.archive.org/web/20130701003854/http://www.scolytid.msu.edu/) contains a worldwide species list of Xyleborini, a major group of ambrosia beetles, from the Catalog of Scolytidae and Platypodidae of S.L. Wood and D.E. Bright (1992)]
- A USDA-sponsored information resource and key (http://itp.lucidcentral.org/id/wbb/xyleborini/) to the world genera of Xyleborini
- American Bark and Ambrosia Beetles (http://www.barkbeetles.info)
- More information on ambrosia beetle social behaviour and fungiculture on [1] (http://behav.zoology.unibe.ch/index.php?pp=55&p=46)
- Farewell to taco topping? (https://web.archive.org/web/20120422080021/http://www.dontmovefirewood.org/blog/farewell-taco-topping.html) The effects of the Redbay ambrosia beetle and laurel wilt disease
- Ambrosia beetles on the UF / IFAS Featured Creatures Web site
 - *Platypus* spp., ambrosia beetles (http://entomology.ifas.ufl.edu/creatures/trees/beetles/platypus.htm)

- *Xylosandrus crassiusculus*, Asian (or granulate) ambrosia beetle (http://entomology.ifas.ufl.edu/creatures/trees/asian_ambrosia_beetle.htm)
- *Xylosandrus compactus*, black twig borer (http://entomology.ifas.ufl.edu/creatures/trees/black_twig_borer.htm)

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Ernobius mollis

Ernobius mollis, known generally as the **pine bark anobiid** or **pine knot borer**, is a species of beetle in the family Ptinidae.[1][2][3][4][5]

Subspecies

These two subspecies belong to the species *Ernobius mollis*:

- *Ernobius mollis espanoli* Johnson, 1975 g
- *Ernobius mollis mollis* (Linnaeus, 1758) g

Data sources: i = ITIS,[1] c = Catalogue of Life,[2] g = GBIF,[3] b = Bugguide.net[4]

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Ernobius mollis



Ernobius mollis sideview

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Ptinidae
Genus:	*Ernobius*
Species:	***E. mollis***

Binomial name

Ernobius mollis
(Linnaeus, 1758)

Synonyms[1]

- *Ernobius consimilis* (Gmelin, 1790)
- *Ernobius convexifrons* (Kugelann, 1792)
- *Ernobius reversus* (Melsheimer, 1846)
- *Ernobius sybaris* Mulsant and Rey, 1863
- *Ernobius tarsatus* Kraatz, 1881
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Pentarthrum huttoni

Pentarthrum huttoni is a species of wood boring weevil in family Curculionidae. It has a mainly nearctic distribution, but has also been reported from several European countries. It was first reported in Austria in 2006 when it was found to be the cause of disintegration of historically significant 18th century softwood coffins in the crypt of St. Michael's church in the center of Vienna.[1]

These beetles prefer extremely high humidity (100%), and also prefer to attack wood that is already rotting. Most Central European records are from buildings.[2]

Pentarthrum huttoni	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Cossoninae
Tribe:	Pentarthrini
Genus:	*Pentarthrum*
Species:	***P. huttoni***
Binomial name	
Pentarthrum huttoni Wollaston, 1854	

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Common furniture beetle

The **common furniture beetle** or **common house borer** (*Anobium punctatum*) is a woodboring beetle. In the larval stage it bores in wood and feeds upon it. Adult *Anobium punctatum* measure 2.7–4.5 millimetres (0.11–0.18 in) in length. They have brown ellipsoidal bodies with a prothorax resembling a monk's cowl .[1]

Common furniture beetle	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Ptinidae
Genus:	*Anobium*
Species:	***A. punctatum***
Binomial name	
Anobium punctatum De Geer, 1774	

Contents

Life cycle

Pest control

See also

References

Life cycle

Adults do not feed; they just reproduce. The female lays her eggs in cracks in wood or inside old exit holes, if available. The eggs hatch after some three weeks, each producing a 1 millimetre (0.039 in) long, creamy white, C-shaped larva. For three to four years the larvae bore semi-randomly through timber, following and eating the starchy part of the wood grain, and grow up to 7 millimetres (0.28 in). They come nearer to the wood surface when ready to pupate. They excavate small spaces just under the wood surface and take up to eight weeks to pupate. The adults then break through the surface, making a 1 mm to 1.5 millimetres (0.059 in) exit hole and spilling dust, the first visible signs of an infestation.

Pest control

The first step in pest control is prevention. Particularly important in this respect is to keep the timber dry - below 16% moisture content. A relative humidity within the building above 60% may lead to an infestation, and timber moisture content below 12% is too dry for an infection to occur.[2] *Anobium punctatum* normally only attacks seasoned sapwood timber, not live or fresh wood. Also, it usually does not attack heartwood timbers. This is readily observed from infested structures, where one piece of timber may be heavily attacked but an adjacent one left virtually untouched according to whether it is made from the heartwood or the sapwood part of a tree trunk. Infestations are also usually a problem of old wooden houses built with untreated timbers. Some building regulations state that timbers with more than 25% sapwood may not be used, so that wood borer infections can not substantially weaken structures.



Woodworm holes and burrows exposed in wooden floorboard

Infection, past or present, is diagnosed by small round exit holes of 1 to 1.5 mm diameter. Active infections feature the appearance of new exit holes and fine wood dust around the holes.

Because of the 3–4 year life cycle of *Anobium punctatum*, timber or timber products bought containing an *A. punctatum* infection may not manifest holes until years after the timber has been acquired. Infestation can be controlled by application of a residual insecticide (such as permethrin) to infected areas, by professional fumigation, or by replacing infected timber .[3] Simple aerosol insecticide sprays will only kill the adult borer on the wing but not the burrowing larvae, which remain relatively protected inside infected timbers. Freezing infected timber, or heating to 50 °C for a day or more, will kill beetle larvae, but offer no residual protection.

See also

- Woodworm

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Deathwatch beetle

The **deathwatch beetle**, *Xestobium rufovillosum*, is a species of woodboring beetle that sometimes infests the structural timbers of old buildings. The adult beetle is brown and measures on average 7 mm (0.3 in) long. Eggs are laid in dark crevices in old wood inside buildings, trees, and inside tunnels left behind by previous larvae.[1] The larvae bore into the timber, feeding for up to ten years before pupating, and later emerging from the wood as adult beetles. Timber that has been damp and is affected by fungal decay is soft enough for the larvae to chew through. They obtain sufficient nourishment by using a number of enzymes present in their gut to digest the cellulose and hemicellulose in the wood.

The larvae of deathwatch beetles weaken the structural timbers of a building by tunneling through them. Treatment with insecticides, used to kill the larvae, is largely ineffective as killing the adult beetles when they emerge in spring and early summer may be a better option. However, infestation by these beetles is often limited to historic buildings, because modern buildings tend to use softwoods for joists and rafters instead of aged oak timbers, which the beetles prefer.

To attract mates, the adult insects create a tapping or ticking sound that can sometimes be heard in the rafters of old buildings on summer nights; therefore, the deathwatch beetle is associated with quiet, sleepless nights and is named for the vigil (watch) being kept beside the dying or dead. By extension, a superstition has grown up that these sounds are an omen of impending death.

Deathwatch beetle



Scientific classification	
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Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Ptinidae
Genus:	*Xestobium*
Species:	***X. rufovillosum***

Binomial name

Xestobium rufovillosum
(De Geer, 1774)

Contents

Taxonomy
Description
Distribution and habitat
Life cycle
Ecology
Host selection
Communication
Mating
Damage
Treatment
In culture
References
External links

Taxonomy

The deathwatch beetle is part of the beetle family Ptinidae, formerly known as Anobiidae. This includes a number of subfamilies including Ptininae, the spider beetles which are mostly scavengers, Anobiinae, wood-boring beetles, and Ernobiinae, deathwatch beetles, also wood-borers. In 1912, Pic erected Ernobiinae for beetles previously classified under Dryophilini by Fall in 1905. White elevated this taxon to subfamily status in 1962 and 1971, and in 1974 included 14 genera in the subfamily.[2]

Description

The eggs are white, slightly pointed at one end and sticky.[3][4] Eggs measure on average 0.7 mm (~0.03 in) in length and 0.5 mm (~0.02 in) in width. [5]

The larvae are creamy-white with six legs, black jaws, a pair of eyespots on either side of the head. They grow to about 11 mm (0.4 in) long making them the largest *Ptininae* found in Britain. These larva are distinctive due to a swollen thoracic region and multiple golden setae [5]

The pupa, when newly formed, is shiny and milky white in colour . They will gradually darken as they mature and produce eyes, tarsi, and “teeth”. During this stage of development, they will completely change appearance by forming a head, complete eyes, mouthparts, antennae, and legs. The pupa measures 7-8 mm in length and around 3 mm in width.[5]

The adult deathwatch beetle is cylindrical measuring on average 6 to 7.5 mm (0.24 to 0.30 in) long. The head is largely concealed by a brown thoracic shield. The shield and elytra are dark brown or reddish-brown, with a patchy felting of yellowish-grey short hairs. The antennae have eleven segments, the distal three segments are somewhat enlarged.[3][4]

Distribution and habitat

This beetle is found in Europe, including the United Kingdom, North America, Corsica, Algeria, and New Caledonia.[6] Its natural habitat is dead or decaying hardwood, or in some cases coniferous wood, especially when the timber has been softened by fungal attack.[6] This may be due to the way fungal decayed wood effects nitrogen metabolism in the deathwatch beetle.[7] Decayed wood is also much easier for the larva of the deathwatch beetle to bore into which allows them to develop at a faster rate.[7] The sapwood is more nutritious and is usually attacked first, followed by heart wood that has been softened by decay. Oak (*Quercus* spp.) is the main host, with American oaks being more susceptible than European oaks. Pollarded willow is also attacked in the United Kingdom. The beetle does not infest wood that has recently died; about sixty years must pass for dead oak to reach a suitable condition for attack.[8] These beetles tend to stay on the same piece of wood for several generations until resources are used up and the piece of wood is no longer sufficient.[9]

Life cycle

In Britain, the adults emerge in April, May or June. The males emerge first, and the females are willing to copulate as soon as they emerge, often in the afternoon.[10] Emergence only occurs in temperatures above 10 degrees Celsius.[11] Mating takes place in a concealed location, mainly on surface wood, and lasts for about an hour. Females lay eggs in crevices in the wood or in the holes left by emerging beetles, The adults do not feed, and so die within a few weeks, by which time the female may have laid 40 to 80 eggs in small batches.[10][11]

The eggs hatch after about a month. The newly hatched larvae are tiny and chew their way into the timber, feeding on the wood. Their growth is slow and it may take from two to ten years, or even more, for them to reach their full size. At this stage they pupate in a chamber close to the wood surface, and either emerge through a newly created hole after twenty to thirty days, or else emerge in the following spring (about eleven months later).[12][10]

Ecology

In buildings, deathwatch beetles infest old oak timbers, especially those that have been the subject of fungal decay, usually by the fungus *Donkioporia expansa*. This fungus affects damp timber, often gaining entry where rafters or joists are embedded in stone walls, or in the vicinity of leaking roofs or overflowing gutters. It is not the adult insects that cause structural damage to the building, but rather their larvae tunneling through the wood.[13]

Wood is difficult to digest, but as long as the wood has been softened by fungal decay, the enzymes in the guts of the larvae are able to digest the cellulose and hemicellulose forming the cell walls; this enables the larvae to make use of the protein, starch and sugars found within the cells.[14]

The steely blue beetle (*Korynetes caeruleus*) is a predator of the deathwatch beetle and of the common furniture beetle (*Anobium punctatum*). The adult female blue beetle lays her eggs in the exit holes made by the emerging borers, and the carnivorous larvae wander through the galleries made by the wood-borers, feeding on their larvae.[15] The adult deathwatch beetles are weak fliers and may run over the surface of the timber, rather than fly. They are sometimes caught by spiders, their silk-encased husks being found on webs.[16]

Host selection

A female deathwatch beetle is short-lived (1-2 months) and must find a suitable host in which to lay her offspring relatively quickly. She is capable of using odor to locate wood that has been decayed by fungi, which provides an excellent host.[17] When selecting a host, old wood (more than a century old) is favoured.[18] Trees with deep crevices are also favoured, as they provide a dark safe shelter for the eggs.[19]

Communication

A deathwatch beetle communicates by hitting its head on a substrate to create a noise, a method called tapping.[20] Males and females differ in that males usually tap first, and females tap only in response to males. A female responds within 2 seconds of a male tap. After the female responds, a male will tap again from 2 to 30 seconds later. The taps create a substrate-borne vibration. This long-distance communication mode differs from that of most wood-boring beetles, which use pheromones.[21]

To locate females, males will walk a short distance, stop and tap, orient themselves towards a female's response and repeat. if females respond they advertise their receptivity. Recently mated females will not respond.[22][21] Each tapping bout contains between 4-11 taps at an average frequency of 10 Hz. [21] Females will only respond to tapping bouts with 6 or more taps and only bouts with a frequency of 4-20 Hz. Males with higher frequencies are more likely to obtain a mate than males with lower frequencies.[22]

Mating

Females have been shown to be selective of which males they mate with. During mating, males give up a significant fraction of their body mass, an average of 13.5%, via ejaculation of the spermatophore. This is a nutritional nuptial gift to the female. Although females cannot tell the mass of the male by looking at them, females can instead determine the mass of the male when the male tries to climb on the females back and mount them. Since male deathwatch beetles do not feed, their resources for the gift have been stored from the larval stage. Males who are heavier in mass are capable of donating a larger percentage of their body mass to the female than lighter males which results in females choosing heavier males and rejecting lighter males. By giving up this much body weight, males are reducing the likelihood that they will mate with an additional female due to a lack of resources for a further gift.[23]

Damage

Due to many English buildings, especially in south England, being built from old oak wood which these beetles seem to be attracted to, the greatest economic damage these beetles have are in England [24][25]

Identification of which insect is present in interior timbers is difficult; by their nature, the larvae are tucked away from sight in their galleries. The presence of wood-boring insects may be indicated by frass (fecal residue) and fresh dust. Recent exit holes often have bright rims, while the rims of older holes have become dull. The species of insects involved can sometimes be identified by examination of the fecal pellets in the frass. Adult beetles, alive or dead, may be present on the glass or the sills of windows, as may the specific enemies of the beetles in the same locations—a likely indication of specific wood-boring insects inside.[26]

Direct examination of the interior of the timber by destructive means is often not acceptable, and non-invasive means are required. Other means of identifying the wood-boring insects include pheromone traps; these are effective for the common furniture beetle and the house longhorn beetle (*Hylotrupes bajulus*) but not for the deathwatch beetle. However, adults of the deathwatch beetle are attracted to light. The sounds of the feeding larvae can be heard either unaided or with the help of a stethoscope, and X-ray scans and computer tomography can also be used. Similarly, active larvae may be identified by vibrations in the ultrasound range.[26] The exit holes of deathwatch beetles are 2 to 3 mm (about 0.1 inch) in diameter, larger than those produced by the common furniture beetle.[27]

When attacking a building, deathwatch beetles will only attack buildings primarily made out of hardwood. Coniferous wood in buildings will be attacked only if it is in contact with the hardwood.[24]

Treatment

This beetle was first described in 1668 by John Wilkins, but it was not until until 1913 that the first scientific study was conducted by Professor Lefroy in an attempt to come up with a management solution for these beetles. [28][29]

The larvae of deathwatch beetle feed deep within timbers. Recent studies have suggested that most of the previously accepted practices of external application of insecticides are largely ineffective. Only gas fumigation remains effective, but poses considerable practical challenges in effectively sealing the larger, historic types of properties that these beetles are mostly attracted to.[30] External insecticide application may, in fact, do more harm than good by killing the natural enemies of the beetle. One way of dealing with the problem may be with the use of ultra-violet "insectocutors", to attract and kill the adults that emerge from the wood in the spring. If there is concern about the strength of structural timbers, a structural surveyor can drill core samples to determine the condition of the wood.[31]

Modern techniques of ultrasound examination now allow the extent and localisation of an attack within timbers to be determined with great accuracy, and, for historic properties where damage to ornate plasterwork must be avoided, can be followed by micro-drilling and highly-targeted injection of insecticide via hypodermic needle. Alternatively, where a degree of damage to the fabric of a building is acceptable, larger 6 mm holes can be drilled deep into the timbers, and a thick, insecticide-laden paste introduced which does not seep out into surrounding areas. In all situations, any structural damage which has permitted water to ingress and moisten the timbers now being attacked should be addressed in order to slow down the life cycle of the insects, and thus minimize their spread.[30]

In culture

The tapping sound of the deathwatch beetle has long been associated as a harbinger of death, being most audible on quiet nights in the rafters of old houses, and in silent bedside vigils for the dying.[32][33]

Its notoriety as an ill omen is alluded to in the fourth book of John Keats' 1818 poem "Endymion":

"*...within ye hear*

No sound so loud as when on curtain'd bier

The death-watch tick is stifled."[34]

("Stifled" because the death it was portending has taken place.)

The term "death watch" has been applied to a variety of other ticking insects, including *Anobium striatum*; some of the so-called booklice of the family Psocidae,[35] and the appropriately named *Atropos divinatoria* and *Clothilla pulsatoria*. (In Greek mythology, Atropos and Clotho were two of the three moirai (Fates) associated with death.)

In 1838 Henry David Thoreau published an essay mentioning the deathwatch beetle. It is possible that this essay influenced Edgar Allan Poe's 1843 short story "The Tell-Tale Heart" and that the sound the protagonist was hearing at the end of that story was that of a beetle tapping inside the wall, not the beating of the (dead) victim's heart.[36] However, it is more likely that it was the metronomic ticking of a booklouse rather than the groups of six to eight taps made by the deathwatch beetle.[35]

The beetle was referenced in Mark Twain's 1876 *The Adventures of Tom Sawyer*: "Next the ghastly ticking of a deathwatch in the wall at the bed's head made Tom shudder – it meant that somebody's days were numbered."[37]

In Dorothy L. Sayers' *Gaudy Night* (chapter 17), the mechanism of the ticking of the death-watch beetle is discussed, and it is compared with a clicking sound made by an ill-fitting hard shirt front.

In 1988, Linda Pastan wrote a poem entitled "The Deathwatch Beetle".[38] In 1995, Alice Hoffman made reference to the deathwatch beetle in her novel *Practical Magic*, using it as an omen of death; whenever anyone hears its clicking, that person soon dies.[39]

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External links

- Deathwatch beetle (https://web.archive.org/web/*/www.arkive.org/xestobium-rufovillosum) media from ARKive
- Death watch beetle tapping on wood (https://web.archive.org/web/20100930162257/http://www.arkive.org/death-watch-beetle/xestobium-rufovillosum/video-09a.html)
- Museumpests.net Death watch beetle factsheet (http://museumpests.net/wp-content/uploads/2014/03/Deathwatch-Beetle.pdf)
- Data related to *Xestobium rufovillosum* at Wikispecies

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Hylotrupes

Hylotrupes is a monotypic genus of woodboring beetles in the family Cerambycidae, the longhorn beetles. The sole species, ***Hylotrupes bajulus***, is known by several common names, including **house longhorn beetle**, **old house borer**,[1] and **European house borer**.[2] It is the only genus in the tribe **Hylotrupini**.

Contents

Distribution
Description
Biology
Gallery
References

Distribution

This species, originating in Europe, and having been spread in timber and wood products, now has a practically cosmopolitan distribution, including Southern Africa, Asia, the Americas, Australia, and much of Europe and the Mediterranean.[3][4]

Description

Hylotrupes bajulus can reach a body length of about 8–20 mm (0.31–0.79 in), while mature larva can reach 30 mm (1.2 in).[3][4] These beetles are brown to black, appearing grey because of a fine grey furriness on most of the upper surface. On the pronotum two conspicuously hairless tubercles are characteristic of the species. On the elytra usually there are two whitish pubescent spots. Females do not have a real ovipositor, only a little more elongated telson. The species can be defined polymorphic, having an extreme variability, both in the dimensions and in the aspect. In small specimens the pubescent spots on the elytra disappear almost completely and the legs and antennae turn to a reddish color.

Biology

Adults are most active in the summer (June–September).[3][4] Only the larvae feed on the wood, with a preference for dead wood of pines (Pinus), fir, spruce (*Picea abies*), Araucaria and Pseudotsuga species .[4][5] The life cycle from egg to beetle typically takes two to ten years,[3] depending on the type of wood, its age and quality, its moisture

Hylotrupes	
	
Hylotrupes bajulus. Male	
	
Female	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Cerambycidae
Subfamily:	Cerambycinae
Genus:	***Hylotrupes***
Species:	***H. bajulus***
Binomial name	
Hylotrupes bajulus (Linnaeus, 1758)	



Mounted specimen

content, and also depending on environmental conditions such as temperature. Larvae usually pupate just beneath the wood surface and eclose in mid to late summer. Once the exoskeleton of the newly emerged adult beetle has hardened sufficiently the adults cut oval exit holes 6–10 mm (¼ to 3/8 in) in diameter, typically leaving coarse, powdery frass in the vicinity of the hole.[6]

0:00 / 0:00

Eating sounds of an Old-house borer

Hylotrupes bajulus preferentially attacks freshly produced sapwood of softwood timber, but can also be found in the sapwood of certain hardwood species such as oak. In softwood such as spruce, it will also attack the heartwood. Contrary to the name "old-house borer", the species is more often found in new houses; maybe because the beetles are attracted to the higher resin content of wood harvested more recently than 10 years earlier. If old wood is attacked, the damage is usually greater. As the nutrient content of wood decreases with age the larva has to consume larger amounts of wood.[7]

In Australia the infection of home construction is mainly caused by the use of wood already infected with the eggs or larvae of the beetles if the wood is not properly kiln-dried in production.[8][9]

Gallery



Larva



Larva exposed in infested wood



Adult. Side view



Front view

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Lyctus brunneus

Lyctus brunneus is a species of beetle in the family Bostrichidae. It is a member of the subfamily Lyctinae, the powderpost beetles. It is known commonly as the **brown powderpost beetle**[1] or **brown lyctus beetle**. Today it is distributed worldwide but it was probably originally native to the Neotropical region.[2]

Like other powderpost beetles, this species lives in wood.[3]

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Lyctus brunneus	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Superfamily:	Bostrichoidea
Family:	Bostrichidae
Subfamily:	Lyctinae
Tribe:	Lyctini
Genus:	*Lyctus*
Species:	***L. brunneus***
Binomial name	
Lyctus brunneus (Stephens, 1830)	

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Wharf borer

The **wharf borer**, *Nacerdes melanura*, belongs to the insect order Coleoptera, the beetles. They belong to the family Oedemeridae, which are commonly known as false blister beetles. Wharf borers are present in all the states of the USA except for Florida. It takes about a year to develop from an egg to an adult. The insect is called the 'wharf borer' because the larval stage of this insect is often found on pilings and timbers of wharves, especially along coastal areas. The adult beetles can be identified via a black band across the end of both elytra, or wing covers. In addition, wharf borers can be distinguished from other members of the family Oedemeridae via the presence of a single spur on the tibia of the forelegs, and the distance between both eyes (twice the length of one eye). Eggs are oviposited on rotten wood where larvae hatch and burrow to feed on rotten wood. Adults do not feed and depend on stored energy reserves accumulated during the larval stage. They are considered to be a pest because they damage wood used in building infrastructures.

Wharf Borer



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Oedemeridae
Genus:	*Nacerdes*
Species:	***N. melanura***

Binomial name

Nacerdes melanura
(Linnaeus, 1758)

Contents

Identification

Natural history

- Distribution and habitat
- Life cycle
- Temperature- and relative humidity-dependent development

Human Impact

References

Identification

The female of this beetle will lay eggs in any damp, decaying timber, which has been attacked by fungus. The eggs are creamy white in colour, slightly curved with tapered ends. The larvae, also creamy white, is equipped with brown mandibles, ready to bore into the timber and feed on the wood. The adult insects are around 10–12 mm in length, yellowish to reddish orange in colour, with a long slender body and antennae half of its body length. The adult beetles can emerge from under the floor of buildings in quite large numbers, causing the occupants to think they may be being invaded by cockroaches. The beetles themselves are quite harmless. They may be distinguished from cockroaches by the black band across the end of both elytra. Another distinguishing feature is the three raised longitudinal lines on each wing case - a feature common to all beetles in the family Oedemeridae. There are only seven species of this family in the UK. In general, in size and form they resemble Soldier Beetles found on flowers.



Wharf borer, *Nacerdes melanura*

Natural history



Wharf borer, *Nacerdes melanura*

Distribution and habitat

This is a cosmopolitan species. They can be found anywhere where there is moist and decaying wood, such as wharf timbers that are regularly submerged by a tidal flow river, for example near the River Thames. A survey by Pitman *et al.* (2003) revealed the wharf borer to be widespread in temperate countries. There were samples recorded in Australia, New Zealand, Japan, France, Denmark and Canada.[1] Pitman *et al.* (2003) further noted that wharf borers are widespread in the UK and Wales, with a few records in Scotland, but neither adults nor larvae were found in Ireland. This beetle is thought to be a native of the Great Lakes region of North America and has been reported to cause much damage to dock timber in this region. However, others believed that they were introduced to the New World from Europe by the lumber trade or by driftwood. There is still uncertainty in the scientific literature about the origin of the wharf borer.[2]

Wharf borer adults may be present in different types of habitats but larvae are almost always restricted to damp, rotten wood. Buried pieces of wood may also harbor the insects. It was said that there was an increase in numbers of this insect in London following the Second World War, when masses of timber became buried under the ground following bomb blasts. They were found beneath the floor of gasoline stations, apartments, and even telegraph poles.[2]

Life cycle

Like all beetles, the wharf borer undergoes complete metamorphosis. The development time from egg to adult is about 12 months, and adults tend to emerge around June to late August in the U.K. Eggs are deposited on wood surfaces where they are subjected to temperature extremes. Egg longevity is reported to be 5–11 days.[1] First instar larvae burrow about 1 cm beneath the surface of the wood after hatching, where soft-rot type degradation is evident.[3] The larval stage is reported to last from up to 2 months to 2 years, during which time larvae digest cellulose and hemicellulose. Larvae produce the enzyme cellulase, which enables them to feed on rooting wood, similar to many wood-boring Coleopterans.[1] Tunnels formed by larvae during burrowing through the wood can be 30 cm long . A certain head capsule size must be attained for larvae to pupate, which takes about 8.5 months to attain.[3] The cream white Pupae are reported to last 6–17 days, the exact amount of time being influenced by temperature and relative humidity. At the onset of pupation, the abdomen is reduced and the head loses its prognathous form. After 3 days, the eyes start to be pigmented, followed by the mandibles at six days and the elytra at nine days. Pupae are capable of moving the abdomen from side to side.[1][3] Adults are short-lived, non-feeding, free-living, able to fly, and can locate wood via olfactory cues. They emerge from the resting pupal stage between May and September, though are more often observed in June. Adults live for about 2–10 days under laboratory conditions,[3] during which time they mate and lay eggs. Females are not substrate specific when choosing an oviposition site. Wharf borers are known to infest both hardwood and softwood.

Temperature- and relative humidity-dependent development

Temperature influences development of eggs, and eggs only develop within the range 20-30 °C. The upper temperature limit for eggs to hatch is approximately 30-35 °C. This may explain the absence of the wharf borer in tropical climates. Relative humidity also influences egg development, with the lower threshold being 20-40%. Females lay eggs at temperatures that are suitable for egg development.[1] Temperature is the most important factor that influences the development of the larva and the pupa. Relative humidity and photoperiods do not adversely affect development. It is important to note that winter does not induce the larvae to pupate. In fact, lower temperatures increase the time for the larvae to attain the required head capsule size for pupation by virtue of a reduced metabolic rate. Adults emerge from the pupal stage at almost all relative humidities. This indicates that the pupal stage is more resistant to desiccation than eggs because, as eggs do not develop at relative humidities lower than 20% . Pupae are

reported not to develop below 10 °C, or above 30 °C.[1] At higher temperatures, adult longevity is greatly reduced. This is because insect activity increases, and therefore speeds up usage of stored energy reserves. Lower relative humidity also decreases longevity due to increased desiccation, especially with non-feeding adults and those without an external supply of water.[1]

Human Impact

The wharf borer's name is of importance to fisherman, sailors, and quarrymen who work along coastal areas. Damage done to old ships and docks by the wharf borer is a good indication of how old the vessels are as the beetles only attack old timber. The presence of wharf borers and the simultaneous destruction can be accepted as a safety precaution to repair docks and ships to avoid dangerous accidents.[1] It is known as a secondary pest, because the larva mainly feed on damp and decaying wood found along waterways and coastlines. The network of tunnels form when wharf borer larvae burrow and ingest the rotten wood, weakening the mechanical support given by the wood.[2] This leads to increased damages in plumbing and rotting timbers. Oak, poplar, and pine are some of the timbers attacked by the wharf borer, indicating its development in both soft and hard woods.[1] It is best to correct the wood moisture problems and remove the source of infected decaying wood. The beetles, generally only a nuisance between June to August, can be controlled by the application of a residual insecticide (such as permethrin). This can be applied to the wall and floor junctions of dwellings and offices. These adults can also be simply vacuumed or picked up and discarded.[4] The larvae is found to be a pest of telegraph poles and fences where dogs have urinated. In Toronto, a large number of adults were discovered in a newspaper office, especially attracted to toilets.[2] In America, Drooz (1953) reported that the insect was responsible for very costly damage to foundations underneath buildings in Milwaukee, Wisconsin.To protect stored archaeological timbers from the damaging effects of wharf borers, a procedure has been developed to control the attacks. The first measure calls for checking the particular area for infestation by the insects. Next, the extent of infestation in the stored timbers is determined. Once the degree of damage has been recorded, the timbers need to be isolated and quarantined. The storage area and the infected timbers are subjected to an appropriate treatment system which is compatible with future conservation treatment systems.[1]

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Deathwatch beetle

The **deathwatch beetle**, *Xestobium rufovillosum*, is a species of woodboring beetle that sometimes infests the structural timbers of old buildings. The adult beetle is brown and measures on average 7 mm (0.3 in) long. Eggs are laid in dark crevices in old wood inside buildings, trees, and inside tunnels left behind by previous larvae.[1] The larvae bore into the timber, feeding for up to ten years before pupating, and later emerging from the wood as adult beetles. Timber that has been damp and is affected by fungal decay is soft enough for the larvae to chew through. They obtain sufficient nourishment by using a number of enzymes present in their gut to digest the cellulose and hemicellulose in the wood.

The larvae of deathwatch beetles weaken the structural timbers of a building by tunneling through them. Treatment with insecticides, used to kill the larvae, is largely ineffective as killing the adult beetles when they emerge in spring and early summer may be a better option. However, infestation by these beetles is often limited to historic buildings, because modern buildings tend to use softwoods for joists and rafters instead of aged oak timbers, which the beetles prefer.

To attract mates, the adult insects create a tapping or ticking sound that can sometimes be heard in the rafters of old buildings on summer nights; therefore, the deathwatch beetle is associated with quiet, sleepless nights and is named for the vigil (watch) being kept beside the dying or dead. By extension, a superstition has grown up that these sounds are an omen of impending death.

Deathwatch beetle



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Ptinidae
Genus:	*Xestobium*
Species:	***X. rufovillosum***

Binomial name

Xestobium rufovillosum
(De Geer, 1774)

Contents

Taxonomy
Description
Distribution and habitat
Life cycle
Ecology
Host selection
Communication
Mating
Damage
Treatment
In culture
References
External links

Taxonomy

The deathwatch beetle is part of the beetle family Ptinidae, formerly known as Anobiidae. This includes a number of subfamilies including Ptininae, the spider beetles which are mostly scavengers, Anobiinae, wood-boring beetles, and Ernobiinae, deathwatch beetles, also wood-borers. In 1912, Pic erected Ernobiinae for beetles previously classified under Dryophilini by Fall in 1905. White elevated this taxon to subfamily status in 1962 and 1971, and in 1974 included 14 genera in the subfamily.[2]

Description

The eggs are white, slightly pointed at one end and sticky.[3][4] Eggs measure on average 0.7 mm (~0.03 in) in length and 0.5 mm (~0.02 in) in width. [5]

The larvae are creamy-white with six legs, black jaws, a pair of eyespots on either side of the head. They grow to about 11 mm (0.4 in) long making them the largest *Ptininae* found in Britain. These larva are distinctive due to a swollen thoracic region and multiple golden setae [5]

The pupa, when newly formed, is shiny and milky white in colour . They will gradually darken as they mature and produce eyes, tarsi, and “teeth”. During this stage of development, they will completely change appearance by forming a head, complete eyes, mouthparts, antennae, and legs. The pupa measures 7-8 mm in length and around 3 mm in width.[5]

The adult deathwatch beetle is cylindrical measuring on average 6 to 7.5 mm (0.24 to 0.30 in) long. The head is largely concealed by a brown thoracic shield. The shield and elytra are dark brown or reddish-brown, with a patchy felting of yellowish-grey short hairs. The antennae have eleven segments, the distal three segments are somewhat enlarged.[3][4]

Distribution and habitat

This beetle is found in Europe, including the United Kingdom, North America, Corsica, Algeria, and New Caledonia.[6] Its natural habitat is dead or decaying hardwood, or in some cases coniferous wood, especially when the timber has been softened by fungal attack.[6] This may be due to the way fungal decayed wood effects nitrogen metabolism in the deathwatch beetle.[7] Decayed wood is also much easier for the larva of the deathwatch beetle to bore into which allows them to develop at a faster rate.[7] The sapwood is more nutritious and is usually attacked first, followed by heart wood that has been softened by decay. Oak (*Quercus* spp.) is the main host, with American oaks being more susceptible than European oaks. Pollarded willow is also attacked in the United Kingdom. The beetle does not infest wood that has recently died; about sixty years must pass for dead oak to reach a suitable condition for attack.[8] These beetles tend to stay on the same piece of wood for several generations until resources are used up and the piece of wood is no longer sufficient.[9]

Life cycle

In Britain, the adults emerge in April, May or June. The males emerge first, and the females are willing to copulate as soon as they emerge, often in the afternoon.[10] Emergence only occurs in temperatures above 10 degrees Celsius.[11] Mating takes place in a concealed location, mainly on surface wood, and lasts for about an hour. Females lay eggs in crevices in the wood or in the holes left by emerging beetles, The adults do not feed, and so die within a few weeks, by which time the female may have laid 40 to 80 eggs in small batches.[10][11]

The eggs hatch after about a month. The newly hatched larvae are tiny and chew their way into the timber, feeding on the wood. Their growth is slow and it may take from two to ten years, or even more, for them to reach their full size. At this stage they pupate in a chamber close to the wood surface, and either emerge through a newly created hole after twenty to thirty days, or else emerge in the following spring (about eleven months later).[12][10]

Ecology

In buildings, deathwatch beetles infest old oak timbers, especially those that have been the subject of fungal decay, usually by the fungus *Donkioporia expansa*. This fungus affects damp timber, often gaining entry where rafters or joists are embedded in stone walls, or in the vicinity of leaking roofs or overflowing gutters. It is not the adult insects that cause structural damage to the building, but rather their larvae tunneling through the wood.[13]

Wood is difficult to digest, but as long as the wood has been softened by fungal decay, the enzymes in the guts of the larvae are able to digest the cellulose and hemicellulose forming the cell walls; this enables the larvae to make use of the protein, starch and sugars found within the cells.[14]

The steely blue beetle (*Korynetes caeruleus*) is a predator of the deathwatch beetle and of the common furniture beetle (*Anobium punctatum*). The adult female blue beetle lays her eggs in the exit holes made by the emerging borers, and the carnivorous larvae wander through the galleries made by the wood-borers, feeding on their larvae.[15] The adult deathwatch beetles are weak fliers and may run over the surface of the timber, rather than fly. They are sometimes caught by spiders, their silk-encased husks being found on webs.[16]

Host selection

A female deathwatch beetle is short-lived (1-2 months) and must find a suitable host in which to lay her offspring relatively quickly. She is capable of using odor to locate wood that has been decayed by fungi, which provides an excellent host.[17] When selecting a host, old wood (more than a century old) is favoured.[18] Trees with deep crevices are also favoured, as they provide a dark safe shelter for the eggs.[19]

Communication

A deathwatch beetle communicates by hitting its head on a substrate to create a noise, a method called tapping.[20] Males and females differ in that males usually tap first, and females tap only in response to males. A female responds within 2 seconds of a male tap. After the female responds, a male will tap again from 2 to 30 seconds later. The taps create a substrate-borne vibration. This long-distance communication mode differs from that of most wood-boring beetles, which use pheromones.[21]

To locate females, males will walk a short distance, stop and tap, orient themselves towards a female's response and repeat. if females respond they advertise their receptivity. Recently mated females will not respond.[22][21] Each tapping bout contains between 4-11 taps at an average frequency of 10 Hz. [21] Females will only respond to tapping bouts with 6 or more taps and only bouts with a frequency of 4-20 Hz. Males with higher frequencies are more likely to obtain a mate than males with lower frequencies.[22]

Mating

Females have been shown to be selective of which males they mate with. During mating, males give up a significant fraction of their body mass, an average of 13.5%, via ejaculation of the spermatophore. This is a nutritional nuptial gift to the female. Although females cannot tell the mass of the male by looking at them, females can instead determine the mass of the male when the male tries to climb on the females back and mount them. Since male deathwatch beetles do not feed, their resources for the gift have been stored from the larval stage. Males who are heavier in mass are capable of donating a larger percentage of their body mass to the female than lighter males which results in females choosing heavier males and rejecting lighter males. By giving up this much body weight, males are reducing the likelihood that they will mate with an additional female due to a lack of resources for a further gift.[23]

Damage

Due to many English buildings, especially in south England, being built from old oak wood which these beetles seem to be attracted to, the greatest economic damage these beetles have are in England [24][25]

Identification of which insect is present in interior timbers is difficult; by their nature, the larvae are tucked away from sight in their galleries. The presence of wood-boring insects may be indicated by frass (fecal residue) and fresh dust. Recent exit holes often have bright rims, while the rims of older holes have become dull. The species of insects involved can sometimes be identified by examination of the fecal pellets in the frass. Adult beetles, alive or dead, may be present on the glass or the sills of windows, as may the specific enemies of the beetles in the same locations—a likely indication of specific wood-boring insects inside.[26]

Direct examination of the interior of the timber by destructive means is often not acceptable, and non-invasive means are required. Other means of identifying the wood-boring insects include pheromone traps; these are effective for the common furniture beetle and the house longhorn beetle (*Hylotrupes bajulus*) but not for the deathwatch beetle. However, adults of the deathwatch beetle are attracted to light. The sounds of the feeding larvae can be heard either unaided or with the help of a stethoscope, and X-ray scans and computer tomography can also be used. Similarly, active larvae may be identified by vibrations in the ultrasound range.[26] The exit holes of deathwatch beetles are 2 to 3 mm (about 0.1 inch) in diameter, larger than those produced by the common furniture beetle.[27]

When attacking a building, deathwatch beetles will only attack buildings primarily made out of hardwood. Coniferous wood in buildings will be attacked only if it is in contact with the hardwood.[24]

Treatment

This beetle was first described in 1668 by John Wilkins, but it was not until until 1913 that the first scientific study was conducted by Professor Lefroy in an attempt to come up with a management solution for these beetles. [28][29]

The larvae of deathwatch beetle feed deep within timbers. Recent studies have suggested that most of the previously accepted practices of external application of insecticides are largely ineffective. Only gas fumigation remains effective, but poses considerable practical challenges in effectively sealing the larger, historic types of properties that these beetles are mostly attracted to.[30] External insecticide application may, in fact, do more harm than good by killing the natural enemies of the beetle. One way of dealing with the problem may be with the use of ultra-violet "insectocutors", to attract and kill the adults that emerge from the wood in the spring. If there is concern about the strength of structural timbers, a structural surveyor can drill core samples to determine the condition of the wood.[31]

Modern techniques of ultrasound examination now allow the extent and localisation of an attack within timbers to be determined with great accuracy, and, for historic properties where damage to ornate plasterwork must be avoided, can be followed by micro-drilling and highly-targeted injection of insecticide via hypodermic needle. Alternatively, where a degree of damage to the fabric of a building is acceptable, larger 6 mm holes can be drilled deep into the timbers, and a thick, insecticide-laden paste introduced which does not seep out into surrounding areas. In all situations, any structural damage which has permitted water to ingress and moisten the timbers now being attacked should be addressed in order to slow down the life cycle of the insects, and thus minimize their spread.[30]

In culture

The tapping sound of the deathwatch beetle has long been associated as a harbinger of death, being most audible on quiet nights in the rafters of old houses, and in silent bedside vigils for the dying.[32][33]

Its notoriety as an ill omen is alluded to in the fourth book of John Keats' 1818 poem "Endymion":

"*...within ye hear*

No sound so loud as when on curtain'd bier

The death-watch tick is stifled."[34]

("Stifled" because the death it was portending has taken place.)

The term "death watch" has been applied to a variety of other ticking insects, including *Anobium striatum*; some of the so-called booklice of the family Psocidae,[35] and the appropriately named *Atropos divinatoria* and *Clothilla pulsatoria*. (In Greek mythology, Atropos and Clotho were two of the three moirai (Fates) associated with death.)

In 1838 Henry David Thoreau published an essay mentioning the deathwatch beetle. It is possible that this essay influenced Edgar Allan Poe's 1843 short story "The Tell-Tale Heart" and that the sound the protagonist was hearing at the end of that story was that of a beetle tapping inside the wall, not the beating of the (dead) victim's heart.[36] However, it is more likely that it was the metronomic ticking of a booklouse rather than the groups of six to eight taps made by the deathwatch beetle.[35]

The beetle was referenced in Mark Twain's 1876 *The Adventures of Tom Sawyer*: "Next the ghastly ticking of a deathwatch in the wall at the bed's head made Tom shudder – it meant that somebody's days were numbered."[37]

In Dorothy L. Sayers' *Gaudy Night* (chapter 17), the mechanism of the ticking of the death-watch beetle is discussed, and it is compared with a clicking sound made by an ill-fitting hard shirt front.

In 1988, Linda Pastan wrote a poem entitled "The Deathwatch Beetle".[38] In 1995, Alice Hoffman made reference to the deathwatch beetle in her novel *Practical Magic*, using it as an omen of death; whenever anyone hears its clicking, that person soon dies.[39]

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External links

- Deathwatch beetle (https://web.archive.org/web/*/www.arkive.org/xestobium-rufovillosum) media from ARKive
- Death watch beetle tapping on wood (https://web.archive.org/web/20100930162257/http://www.arkive.org/death-watch-beetle/xestobium-rufovillosum/video-09a.html)
- Museumpests.net Death watch beetle factsheet (http://museumpests.net/wp-content/uploads/2014/03/Deathwatch-Beetle.pdf)
- Data related to *Xestobium rufovillosum* at Wikispecies

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Weevil

Weevils are a type of beetle belonging to the superfamily **Curculionoidea**. They are usually small, less than 6 mm (0.24 in), and herbivorous. About 97,000 species of weevils are known. They belong to several families, with most of them in the family Curculionidae (the true weevils). Some other beetles, although not closely related, bear the name "weevil", such as the biscuit weevil (*Stegobium paniceum*), which belongs to the family Ptinidae.

Many weevils are considered pests because of their ability to damage and kill crops. The grain or wheat weevil (*Sitophilus granarius*) damages stored grain. The boll weevil (*Anthonomus grandis*) attacks cotton crops; it lays its eggs inside cotton bolls and the larvae eat their way out. Other weevils are used for biological control of invasive plants.

Some weevils have the ability to fly, such as the rice weevil.[1][2]

One species of weevil, *Austroplatypus incompertus*, exhibits eusociality, one of the few insects outside the Hymenoptera and the Isoptera to do so.

Weevils



Lixus angustatus

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Suborder:	Polyphaga
Infraorder:	Cucujiformia
Superfamily:	**Curculionoidea** Latreille, 1802

Families

Anthribidae—fungus weevils
Attelabidae—leaf rolling weevils
Belidae—primitive weevils
Brentidae—straight snout weevils
Caridae
Curculionidae—true weevils
Nemonychidae—pine flower weevils

Contents

Taxonomy
Sexual dimorphism
Phylogeny
Gallery
References
Further reading
External links

Taxonomy

Because so many species exist in such diversity, the higher classification of weevils is in a state of flux. They are generally divided into two major divisions, the Orthoceri or primitive weevils, and the Gonatoceri or true weevils (Curculionidae). E. C. Zimmerman proposed a third division, the Heteromorphi, for several intermediate forms.[3] Primitive weevils are distinguished by having straight antennae, while true weevils have elbowed (geniculate) antennae. The elbow occurs at the end of the scape (first antennal segment) in true weevils, and the scape is usually much longer than the other antennal segments. Some exceptions occur. Nanophyini are primitive weevils (with very long trochanters), but have long scapes and geniculate antennae. From the true weevils, Gonipterinae and *Ramphus* have short scapes and little or no elbow.

The most recent classification system to family level was provided by Kuschel,[4] with updates from Marvaldi *et al*.,[5] and was achieved using phylogenetic analyses. The accepted families are the primitive weevils, Anthribidae, Attelabidae, Belidae, Brentidae, Caridae, and Nemonychidae, and the true weevils Curculionidae. Most other weevil families were demoted to subfamilies or tribes. Weevil species radiation was shown to follow steps in plant evolution upon which the weevils feed; they can vary in color from black to light brown.

Some of the features used to distinguish weevil families are:

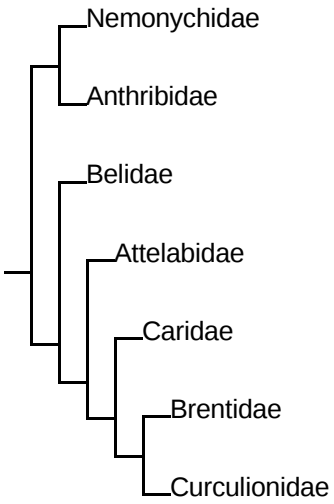
Labrum visible as separate segment to clypeus	Anthribidae, Nemonychidae
Antennae elbowed	most Curculionidae, Nanophyini (Apioninae)
Trochanters (segment between coxae and femora) as long or longer than coxae	Apioninae including Nanophyini
Fore tibia with comb of setae in apical groove opposite tarsal articulation	Belidae
Elytra striate (with longitudinal ridges or grooves)	Brentidae, Curculionidae, Rhinorhynchinae
Rostrum short and broad	Anthribidae, some Curculionidae (some Brachycerinae including *Ithycerus* (New York weevil), Scolytinae and Platypodinae).
Maxillary palps long and projecting (visible from above at tip of rostrum)	Anthribidae, Nemonychidae
Abdominal tergites 6 and 7 without spiracles	Caridae
Gular suture (on ventral part of head) single not double	Attelabidae, Brentidae, Curculionidae.

Sexual dimorphism

Rhopalapion longirostre exhibits an extreme case of sexual dimorphism. The female rostrum is twice as long and its surface is smoother than in the male. The female bores egg channels into the buds of *Alcea rosea*. Thus, the dimorphism is not attributed to sexual selection. It is a response to ecological demands of egg deposition.[6]

Phylogeny

A phylogeny of the Curculionoidae based on 18S ribosomal DNA and morphological data is suggested below:[5]



Gallery



Chrysolopus spectabilis



Rhinotia hemistictus



Rhinotia haemoptera



Lixus scrobicollis



Lixus angustatus



Lixus iridis



Lixus junci



Diaprepes abbreviatus



Phyllobius calcaratus



Gonipterus scutellatus



Aades cultratus



Cyphocleonus achates



Liparus glabiostris



Rhynchites bicolor



Apion (Rhopalapion) longirostre



Apion frumentarium



Hypera zoilus



Sitona macularius



Sitona gressorius



Curculio glandium



Curculio nucum



Curculio elephas



Polydrusus mollis



Phyllobius glaucus



Apoderus coryli



Orychodes indus



Platystomos albinus



Meganthribus pupa



Sitophilus oryzae



Anthonomus rubi



Gonipterus gibberus



Larinus planus



Hylobius abietis



Rhynchophorus cruentatus



Cyrtepistomus castaneus



Cionus hortulanus



Hylobius (Callirus) pinastri



Vanapa oberthuri



Trachelophorus giraffe



Rhigus nigrosparsus



Phyllerythrurus sanguinolentus



Rhinostomus barbirostris



Hypera rumicis larva



Rhinorhynchus rufulus

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External links

- Media related to Curculionidae at Wikimedia Commons

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Maize weevil

The **maize weevil** (*Sitophilus zeamais*), known in the United States as the **greater rice weevil,**[1][2] is a species of beetle in the family Curculionidae. It can be found in numerous tropical areas around the world, and in the United States, and is a major pest of maize.[3] This species attacks both standing crops and stored cereal products, including wheat, rice, sorghum,[4][5][6] oats, barley, rye, buckwheat,[6] peas, and cottonseed. The maize weevil also infests other types of stored, processed cereal products such as pasta, cassava,[5] and various coarse, milled grains. It has even been known to attack fruit while in storage, such as apples.[7]

Contents

Description
Distribution
Life cycle
Host range
Damage and detection
See also
References
Further reading
External links

Description

A close relative of the rice weevil,[6] the maize weevil has a length of 2.5 mm to 4 mm.[1][2] This small, brown weevil has four reddish-brown spots on the wing covers (elytra). It has a long, thin snout, and elbowed antennae.[6] *Sitophilus zeamais* appears similar to the rice weevil (*Sitophilus oryzae*), but has more clearly marked spots on the wing covers, and is somewhat larger.[2] It is able to fly.[6]

Although the maize weevil and rice weevil do look alike, and are easily confused with one another, there are several distinguishing features:[7]

Maize weevil

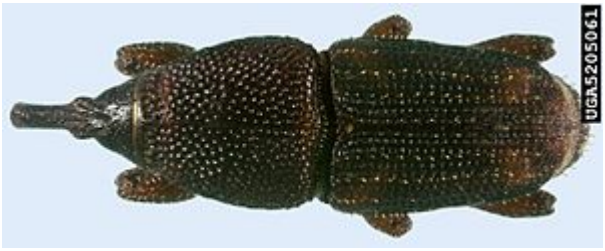
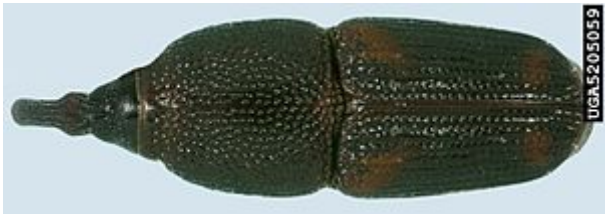


Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Dryophthorinae
Genus:	*Sitophilus*
Species:	***S. zeamais***

Binomial name

Sitophilus zeamais
(Motschulsky), 1855

Maize weevil (*S. zeamais*)	Rice weevil (*S. oryzae*)
	
	
Circular punctures on pronotal dorsum	Longitudinally elliptical punctures on pronotal dorsum
Pronotal punctures have no median puncture-free area and are nearly equally spaced apart	Pronotal punctures are separated by a flat, median, longitudinal puncture-free zone
More than 20 pronotal punctures along the approximate midline, running from neck to scutellum	Less than 20 pronotal punctures along the approximate midline, running from neck to scutellum
Scutellar elevations relatively farther apart compared to their longitudinal length	Scutellar elevations relatively closer together compare to their longitudinal length
Scutellar elevations extend longitudinally approximately halfway down the scutellum	Scutellar elevations extend longitudinally approximately more than halfway down the scutellum
Proepimera meets behind the forecasting coxae and has a barely discernible notch along the posterior edge at the site of the meeting point	Proepimera meets behind the fore coxae and along the posterior edge, has a distinct curved notch
Aedeagus has two dorsal, longitudinal grooves	Aedeagus (in males) is smooth and shiny on the dorsal surface

Distribution

S. zeamais occurs throughout warm, humid regions around the world, especially in locations where maize is grown,[2] including: Polynesia, Argentina, Brazil, Burma, Cambodia, Greece, Japan, Morocco, Spain, Syria, Turkey, United States, USSR, Sub Saharan Africa and Yugoslavia. It is also widely distributed throughout agricultural areas of northern Australia.[7] This species has also been recorded in Canada, in the provinces of Ontario and Quebec,[6] and has been intercepted at ports, but is not well established there. It has, however, been present for several years in Montreal, where grain from the U.S. is stored.[8]

Life cycle

The complete development time for the life cycle of this species averages 36 days.[7] The female chews through the surface of the grain, creating a hole. She then deposits a small oval white egg, and covers the hole as the ovipositor is removed, with a waxy secretion that creates a plug.[6] The plug quickly hardens, and leaves a small raised area on the seed surface. This provides the only visible evidence that the kernel is infested.[7] Only one egg is laid inside each grain. When the egg hatches into a white,

legless grub, it will remain inside and begin feeding on the grain. The larvae will pupate while inside, then chew a circular exit hole,[1] and emerge as an adult beetle. A single female may lay 300 to 400 eggs during her lifetime. Adults can live for 5 to 8 months.[2] Breeding conditions require temperatures between 15 and 34 °C and40% relative humidity.

When the adults emerge, the females move to a high surface and release sex pheromones. Males are then attracted to this pheromone.[7]

Host range

The maize weevil commonly attacks standing crops, in particular, maize before harvest, and is also commonly associated with rice. It infests raw or processed cereals such as wheat, oats, barley, sorghum, rye and buckwheat. It can breed in crops with a moisture content of a much wider range than *S. oryzae*, and has been found in fruit, such as apples during storage. Although the maize weevil cannot readily breed in finely processed grains, it can easily breed in products such as macaroni and noodles, and milled cereals that have been exposed to excessive moisture.[7]

Damage and detection

Early detection of infestation is difficult. As *S. zeamais* larvae feed on the interior of individual grains, often leaving only the hulls, a flour-like grain dust, mixed with frass is evident. Infested grains contain holes through which adults have emerged. A possible indication of infestation is grain, when placed in water, floating to the surface.[7] Ragged holes in individual grains, similar to damage caused by the rice weevil and granary weevil, may indicate infestation.[6] In large stores of grain, an increase in temperature may be detected. The most obvious sign of infestation is the emergence of adults. One study recorded, 5 weeks after infestation, the emergence of 100 adults per kg per day.[1]



Maize damaged by maize weevil larvae

See also

- Granary weevil, also known as the wheat weevil (*S. granarius*)
- Rice weevil (*S. oryzae*)
- Home stored product entomology
- Invasive species
- List of common household pests
- Pest control

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External links

- Images (http://www.invasive.org/search/action.cfm?q=Sitophilus%20zeamais)
- USDA study on temperature management of the maize weevil (http://ddr.nal.usda.gov/bitstream/10113/13133/1/IND20551576.pdf)
- USDA study on contest behaviour of maize weevil larvae when competing within seeds (http://www.ars.usda.gov/sp2userfiles/place/54300530/pdf/1081_AnBe_79.281.pdf)
- African Journal of Biotechnology: Laboratory evaluation of four medicinal plants as protectants against the maize weevil (http://ajol.info/index.php/ajb/article/viewFile/55935/44391)

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Rice weevil

The **rice weevil** (*Sitophilus oryzae*) is a stored product pest which attacks several crops, including wheat, rice, and maize.

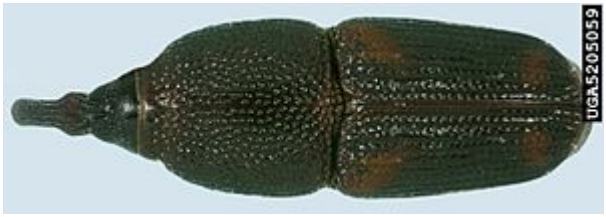
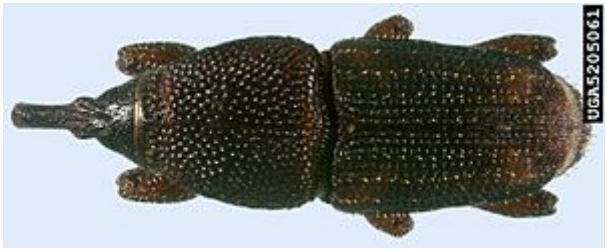
Contents

Description
Biology
Control
See also
References

Description

The adults are around 2 mm long with a long snout. The body color appears to be brown/black, but on close examination, four orange/red spots are arranged in a cross on the wing covers. It is easily confused with the similar looking maize weevil, but there are several distinguishing features:[2]

Rice weevil	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Dryophthorinae
Genus:	*Sitophilus*
Species:	***S. oryzae***
Binomial name	
Sitophilus oryzae (Linnaeus, 1763) [1]	

Rice weevil (*S. oryzae*)	Maize weevil (*S. zeamais*) family :
	
	
Longitudinally elliptical punctures on pronotal dorsum	Circular punctures on pronotal dorsum
Pronotal punctures are separated by a flat, median, longitudinal puncture-free zone	Pronotal punctures have no median puncture-free area and are nearly equally spaced apart
Less than 20 pronotal punctures along the approximate midline, running from neck to scutellum	More than 20 pronotal punctures along the approximate midline, running from neck to scutellum
Scutellar elevations relatively closer together compare to their longitudinal length	Scutellar elevations relatively farther apart compared to their longitudinal length
Scutellar elevations extend longitudinally approximately more than halfway down the scutellum	Scutellar elevations extend longitudinally approximately halfway down the scutellum
Proepimera meets behind the fore coxae and along the posterior edge, has a distinct curved notch	Proepimera meets behind the fore coxae and has a barely discernible notch along the posterior edge at the site of the meeting point
Aedeagus (in males) is smooth and shiny on the dorsal surface	Aedeagus has two dorsal, longitudinal grooves

Biology

Adult rice weevils are able to fly,[3] and can live for up to two years. Females lay 2-6 eggs per day and up to 300 over their lifetime. The female uses strong mandibles to chew a hole into a grain kernel after which she deposits a single egg within the hole, sealing it with secretions from her ovipositor. The larva develops within the grain, hollowing it out while feeding. It then pupates within the grain kernel and emerges 2–4 days after eclosion.

Male *S. orzyae* produce an aggregation pheromone called sitophilure ((4S,5R)-5-Hydroxy-4-methylheptan-3-one) to which males and females are drawn. A synthetic version is available which attracts rice weevils, maize weevils and grain weevils. Females produce a pheromone which attracts only males.

Control

Control of weevils involves locating and removing all potentially infested food sources. Rice weevils in all stages of development can be killed by freezing infested food below 0 °F (-18 °C) for a period of three days, or heating to 60 °C (140 °F) for a period of 15 minutes.[4]



An adult emerges from inside a grain of rice

See also

- Granary weevil (*Sitophilus granarius*)
- Maize weevil (*Sitophilus zeamais*)

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Carpet beetle

Carpet beetle may refer to any of several taxa of beetles:

- some genera of the Dermestidae, a beetle family, including:
 - genus *Attagenus*
 - black carpet beetle, *Attagenus unicolor*
 - brown carpet beetle, *Attagenus smirnovi*
 - *Attagenus pellio*
 - genus *Anthrenus*
 - varied carpet beetle, *Anthrenus verbasci*
 - *Anthrenus scrophulariae*, also known as the common carpet beetle
 - *Anthrenus flavipes* (A. flavipes), also known as the furniture carpet beetle

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Black carpet beetle

The **black carpet beetle** (*Attagenus unicolor*) is a 3–5-millimetre-long (0.12–0.20 in) beetle that can be a serious household pest. The larvae grow to 7 mm (0.28 in) in length, are reddish brown in colour and covered with bristles. The larval form feeds on natural fibres, damaging carpets, furniture and clothing.

Black carpet beetle	
	
adult beetle	
	
Larvae	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Dermestidae
Genus:	*Attagenus*
Species:	***A. unicolor***
Binomial name	
Attagenus unicolor (Brahm, 1791)	

Life cycle

Attagenus unicolor undergoes complete metamorphosis, which has four life stages: Egg, larvae, pupae and adult. Each stage looks different, and needs different amounts of time to reach the next stage.

Eggs are usually laid near or on a food source. If no food source can be found, the female will lay them in dark undisturbed locations where the larvae can feed on carpeting or clothing. They will also lay eggs on or near dog food or other pet food. Eggs take anywhere from 5 to 20 days to hatch depending on the conditions, such as temperature and humidity.

Larvae are about 1 mm (0.039 in) in size when they hatch from the egg. They grow fairly quickly depending on the food source availability and protein found in the food itself. Larvae moult about 10 to 15 times, or more depending on conditions. Sometimes if food is scarce they will retro-moult with the larvae moulting into a lower instar. They can do this multiple times, if they are large enough.

The larval stage is the longest and most destructive stage; they can remain as larvae for up to 3 years, although it does not typically take longer than 3 months to go through the larval stage if food and conditions are good. Larvae pupate in undisturbed locations, far away from the food source so that they aren't cannibalized.

Pupae are cream white but quickly turn yellow and darken with age. They do not eat in this stage nor move. They transform into the beetles in about 8 to 20 days, depending on the conditions. The beetle may stay in the shedded pupae case for an additional day or two.

Beetles start out white but darken with age. They typically do not eat, although they will sometimes eat flower pollen in the wild, but not indoors. Adults live for a few weeks, just long enough to mate and lay more eggs. They are eventually black in colour, hence the name Black Carpet Beetle. Females are capable of laying 50 to 100 eggs.

The whole life cycle under ideal conditions takes about 4 to 5 months, or less if given protein-rich food, such as pet food. The adult females will lay more eggs if water is present in small amounts.

See also

- Varied carpet beetle

External links

- Black carpet beetle (http://entnemdept.ifas.ufl.edu/creatures/fabric/black_carpet_beetle.htm) on the UF / IFAS Featured Creatures website
- Black carpet beetle fact sheet (http://ento.psu.edu/extension/factsheets/black-carpet-beetle), Penn State College of Agricultural Sciences

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Attagenus smirnovi

The **brown carpet beetle**, ***Attagenus smirnovi***, is a beetle from the family Dermestidae. It is a synanthropic pest which lives in human buildings, homes and museums and eats wool-textiles, carpets, skin and fur.[1] Due to its specific epithet *smirnovi*, the beetle is also known in the United Kingdom as the 'Vodka beetle', after the Smirnoff brand of vodka.[2]

Attagenus smirnovi	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Dermestidae
Genus:	*Attagenus*
Species:	***A. smirnovi***
Binomial name	
Attagenus smirnovi Zhantiev, 1973	

Contents

Features
Distribution
References
External links

Features

Their bodies reach a length of between 2.3 and 4 millimetres.[3] The head and pronotum are dark brown to black. Their elytra are densely hairy and light brown.

Distribution

Naturally found in Africa, they have spread to Russia (where they were first observed in 1961, in Moscow, by E. S. Smirnov), the Czech Republic and other eastern European countries, along with Germany (where the first example was found in 1985 in Mecklenburg-Vorpommern), Denmark and the United Kingdom. The species was first described as a new one in 1973, by Rustem Devletovich Zhantiev, who named it *Attagenus smirnovi*. The museums and scientific institutions of Northern Europe set up an international project to research the brown fur beetle's distribution in Europe and how this may be related to climate change.[4] Its research areas include which climatic conditions allow it to spread by flying from house to house.

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External links

- *Attagenus smirnovi* (http://www.faunaeur.org/full_results.php?id=118740) at Fauna Europaea
- Insect pests and climate change. The *Attagenus smirnovi* project. (https://web.archive.org/web/20110719130133/http://smirnovi.natmus.dk/)
- (in German) *Attagenus smirnovi* (http://www.insektoid.info/kaefer/pelzkaefer/#bid372) Images at Insektoid.Info
- (in German) *Attagenus smirnovi* (https://web.archive.org/web/20100520022414/http://www.laves.niedersachsen.de/master/C38832302_L20_D0_I826_h1.html) Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit

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Attagenus pellio

Attagenus pellio, the **fur beetle** or **carpet beetle**, is an important pest damaging stored products such as furs, skins, textiles and grain.

Attagenus pelio is a 4–6 mm-long oval shaped insect with two patches of white hair on the elytra.

See also

Home stored product entomology

References

- Granousky TA. 1997. *Stored Product Pests*. *In Handbook of Pest Control*, 8th Ed. Hedges SA, Moreland D (editors). Mallis Handbook and Technical Training Company

External links

- Dermestidae of the World (http://www.dermestidae.com/Attagenus pellio.html) Habitus and antennae of the male.

Carpet Beetle	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Dermestidae
Genus:	*Attagenus*
Species:	***A. pellio***
Binomial name	
Attagenus pellio (Linnaeus, 1758)	

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Home-stored product entomology

Home stored product entomology is the study of insects which infest foodstuffs stored in the home. It deals with the prevention, detection and eradication of the pests. The five major categories of insects considered in this article are flour beetles, the drugstore beetle, the sawtoothed grain beetle, the Indian meal moth and fruit flies.

This is an important branch of forensic entomology because consumers who find contaminated products may choose to take legal action against the producers. Suitably qualified entomologists are likely to be able to determine the identity of contaminant species, even when no insects are found and the only evidence of infestation is the resulting damage. They should also be able to determine whether the foodstuff was contaminated before or after purchase.

In the United States, companies are required by the U.S. Food and Drug Administration (FDA) to have no more than a certain number of larvae, insects or insect fragments in their products; when this defect action level is exceeded, a consumer can pursue legal remedies.

Contents

Five major stored product pests
- Flour beetles (*Tribolium castaneum* and *Tribolium confusum*)
- Drugstore beetle (*Stegobium paniceum*)
- Sawtoothed grain beetle (*Oryzaephilus surinamensis*)
- Indian meal moth (*Plodia interpunctella*)
- Fruit flies (*Drosophila melanogaster*)

Detection of an infestation
- Red flour beetle detection
- Sawtoothed grain beetle detection
- Drugstore beetle detection
- Indian meal moth detection
- Fruit fly detection

FDA regulations

Prevention and eradication
- Prevention
- Eradication

Conclusion

See also

References

Further reading

External links

Five major stored product pests

Flour beetles (*Tribolium castaneum* and *Tribolium confusum*)



Red flour beetle

Two different types of beetles are classified as flour beetles: the red flour beetle and the confused flour beetle. Both are similar in physical characteristics. They are flat and oval in shape and usually range around 1/8 inch long. Their exoskeletons are reddish brown with a shiny and smooth texture. The eggs, larvae, and pupae resemble each other closely in physical features, as well. The eggs usually tend to be a white color, or at times even colorless. They are very small in size and have a sticky outer covering that causes certain food particles to stick to them. The larvae have six legs, with two pointy projections toward the caudal end. Finally, the pupal stage (a cocoon-like form) is usually a white or brownish color. The beetle life cycle lasts about three years or more, with the larval stage ranging anywhere from 20 to over 100 days, and the pupal stage around eight days. Beetles usually breed in damaged grain, grain dust, high-moisture wheat kernels and flour. The female flour beetle can lay between 300 and 400 eggs during her lifetime [a period of 5 to 8 months]. The flour beetles mainly infest grains, including, but not limited to: cereal, corn meal oats, rice, flour, and crackers. This type of beetle is the most abundant insect pest of flour mills across the United States. Their small size allows them to maneuver through cracks and crevices and get into the home and other areas. Once they are present in areas with potential food sources, they can infest material such as flour, resulting in a sharp odor or moldy flavor. The red flour beetle is able to fly short distances and the confused flour beetle is unable to fly. While the confused flour beetle is more commonly found in the northern United States, the red flour beetles are more predominant in the southern United States in areas with warmer climates.[1]

The red flour beetle and the confused flour beetle are commonly used as a model organisms, to study genetics and ecology. The genome of the red flour beetle has been sequenced.[2]



Tribolium castaneum

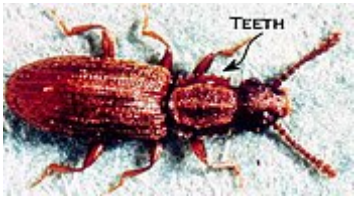
Drugstore beetle (*Stegobium paniceum*)



Drugstore beetle

This beetle is related to the commonly known cigarette beetle. Adult drugstore beetles are cylindrical with lengths ranging from 2.25 to 3.5 mm. They are a reddish-brown color and have elytra, sclerotized (hardened) wings that fold back over the abdomen and hinge upwards, allowing the hind wings to come out to fly. Females are capable of laying up to 75 eggs during a 13- to 65-day period. After the eggs are laid, they hatch into a larval period that can range anywhere from four to 20 weeks. After the larval period, drugstore beetle larvae move out of the substrate to build a cocoon and pupate. The pupation period takes a total of 12–18 days. The entire life cycle of the drugstore beetle lasts approximately two months, but can be as long as seven months. These stored product pests will infest almost anything readily available. Food products prone to infestation include: flours, dry mixes, breads, cookies and other spices. Nonfood material includes: wool, hair, leather and museum specimens. This specific type of beetle has symbiotic yeasts that produce B vitamins, which allow the beetle to survive even when consuming foods of low nutritional value. They are found in areas that have a warmer climate, yet are less plentiful in the tropics than the cigarette beetle.[3]

Sawtoothed grain beetle (*Oryzaephilus surinamensis*)



Sawtoothed grain beetle

The sawtoothed grain beetle is closely related to the merchant grain beetle, and is commonly found in kitchen cabinets feeding on items such as cereal, breakfast foods, dried fruits, macaroni, crackers, etc. They are the most common grain and stored product pest in the United States. They are very active and tend to crawl rapidly while searching for food.[4] They are small insects, reaching a length of about 1/8 of an inch. Their name originates from their distinguishable, sawtooth-like projections found on each side of the thorax. The body of the beetle is flat and slender in shape, and brown in color. The size and shape of the mandibles allow the beetles to easily break through well-sealed packaged foods. An adult female can lay between 45 and 250 eggs that usually hatch within three to 17 days. The larvae have a caterpillar-like appearance, with a yellowish coloration to the body and a brown head. The larval period can last as long as 10 weeks, but can be as short as two weeks. Following the larval instars is the pupal period, which can last one to three weeks. The pupal stage is characterized by the unique process by which these beetles stick together pieces of food material to form protective coverings around their bodies. A fully mature adult beetle, under optimal conditions, can live a maximum of four years, a long lifespan for an arthropod.[5]

Indian meal moth (*Plodia interpunctella*)


Indianmeal moth

Indianmeal moths can infest a variety of foods found in the home. Coarsely ground grains, cereals, dried fruits, and herbs are common items the moths have been known to infest. They have also been found in animal feeds, such as dry dog food, fish food and even bird seed. Adult moths are small; generally, their length averages about 3/8 inch, with a 5/8 inch wing span. As adults, the moths are easily identified by an overall grayish, dirty complexion. However, the wing tips have a bronze color that helps differentiate this particular moth from other household moths. The adults have a distinct forewing pattern, as well, which consists of a light-colored base with about two-thirds of the distal area a red to copper color.[6] The larval stage, or caterpillar, is characterized by a pinkish or yellowish-green body color with a dark brown head. The larval stage of the moth's life cycle is centered on food sources; during the last instar, these larvae are characterized by a movement towards a protected area to pupate. These caterpillars have the capacity to chew through plastic packaging and will often produce silk that loosely binds to food fragments. The pupal stage is generally observed as tiny cocoons that hang from the ceiling; these cocoons can also be found on walls, as well as near the food source. A female can lay over 200 eggs and will usually die after this process because adults Indian meal moths do not eat.[7]

Fruit flies (*Drosophila melanogaster*)


Fruit Fly

Fruit flies are found near ripened or fermenting fruit. Tomatoes, melons, squash, grapes and other perishable items brought in from the garden are a common cause of an indoor infestation. Fruit flies can also be attracted to rotting bananas, potatoes, onions and other unrefrigerated produce purchased at the grocery store and taken home. The body of the fruit fly is tan towards the front part of the body and black towards the rear. They usually have red eyes and are about 1/8 inch long. Females have the ability to lay over 500 eggs, usually in fermenting fruit as a food source. The only environment necessary for successful reproduction is a moist film and fermenting material. Generally, fruit flies are a problem during late summer and fall due to their attraction to ripening and fermenting fruits and vegetables. The entire life cycle can be completed in about a week. Rarely, because of their ability to fly in and out of the home through windows and screens, they have the capability of contaminating food with bacteria and disease-producing organisms.[8]

Detection of an infestation

Careful observation is necessary when detecting the cause of an insect infestation. Each of the five different insects discussed has a unique pattern of destruction. These observations are imperative, as there are not always larvae, pupae, or adults readily available for examination and identification. In the absence of physical specimens, conclusions can be drawn about the probable insect infesting the product just by noting the damage done to the particular food. By noting the type of food and the damage done, a nearly accurate conclusion can be drawn about the type of insect causing the damage, allowing a conjecture about the type of control needed. Having an insect specimen and accurately identifying it can lead to eradication, and ultimately, prevention.

Foods commonly infested include:

- Whole or cracked grains (rice)
- Flour, meal, or similar ground grain products
- Spices
- Cereals
- Pasta
- Candy
- Powdered milk
- Nuts (whole or pieces)

Other items include, but are not limited to: Rodent baits (that contain grain as a feeding attractant), dry pet food, bird seed, grass seed, some powdered soap detergents, dried flowers, potpourri, items stuffed with dried beans or other plant material, and tobacco products.

To identify an insect, and consequently make a decision about the type of control to be implemented, the type of food must first be noted, especially in the absence of a specimen. Although identifying the food is a general start to begin to identify the insect, it must be remembered that it is not always the most accurate method, but is mostly used as a guideline, as some insects are more likely than others to be found in certain types of grain, flour, etc. The type of food is not always conclusive to the type of insect found in it, as insects are not extremely picky, and many families and species are found on a wide range of different foodstuffs. Using the infested item as a guideline, noting the type of damage done to the product is the next step. Some insects, like the drugstore beetle, leave telltale tiny holes in the damaged product, while Indianmeal moths are notorious for the spider web-like threads left behind in the food they infest. These observations can generally lead to a mostly accurate conclusion about the type of insects causing the damage, but obviously the most accurate conclusion relies on any specimen found either directly in the stored product or in the vicinity. The larvae, pupae, and adults can be found directly in the product while usually only the pupae and adults are found in the vicinity of the product. It is not practical to assume any person has knowledge of general entomology, so the following analysis focuses on the five major pests that most commonly infest stored products, beginning with the type of foods infested, signs indicative of a particular insect infestation, and a description of the larvae, pupae, and adults, including behavior, as well as appearance.

Red flour beetle detection

This beetle is similar to the saw-toothed grain beetles in both habits and types of products infested. It is a serious pest in flour mills and wherever cereal products and other dried products are stored and/or processed. Generally, the beetle is attracted to grain with a high moisture content, and usually causes the grain to acquire a grayish tint. The beetle may also impart a bad odor, which then affects the taste of the infested products, as well as encouraging the growth of mold in the grain. This foul odor and taste in the various food products are caused by pheromones and toxic quinone compounds.[9]

Sawtoothed grain beetle detection

The sawtoothed grain beetle feeds on a plethora of feeds, but is not capable of attacking whole or undamaged grains; therefore, the larvae are commonly found in processed grains (flour and meal), dry dog food, dried fruits, candy bars, tobacco, drugs, dried meats, and a variety of other stored food products.[10][11]



Damage caused by red flour beetles

Drugstore beetle detection

These beetles will infest almost anything- they are found most often, however, in flour, bread, spices, breakfast foods, and meal. In the case of an infestation, contaminated products have telltale tunnels which have the appearance of tiny holes. These beetles do not sting, bite, or harm pets or damage a house, yet have the potential, in large infestations, to become a nuisance by flying on doors and windows in heavy populations.

Indian meal moth detection

Indian meal moths infest both cereal and stored grain products, packaged goods, and surface layers of shelled corn. The most telltale sign of the Indian meal moth is the silk webbing the larvae (caterpillars) produce when feeding on the surfaces of foods. This silk webbing may appear to be or resemble cobwebs inside the products' containers. Often, a few larvae may be found in the packaging of the product, along with the ‘cobwebs’, cast skins and frass.

Larvae are white worms with black heads, which, when ready to pupate, crawl up the walls of the home in most cases, and are suspended from the ceiling attached by a single silken thread. Most complaints about these moths come during the warmer parts of the year- usually July through August- but the moths can appear during any month. As with all insects important to stored product entomology, it cannot be automatically assumed that products were previously infested, yet, it is more common for these moths to contaminate products before purchase than for the moth to fly into a home through open windows or doors. An important aspect of the Indian meal moth is that the larva is the only stage of the insect's life cycle to feed on stored products, the adults do not.

Fruit fly detection



A fruit fly larva feeding on a cherry

Fruit flies are attracted to ripened fruits and vegetables, usually in the kitchen area, but will breed in garbage disposals, empty bottles and cans, wet or damp mops or cleaning rags, and trash containers. The only requirement for these flies to breed is a moist film of fermenting material. Infestations can originate from over-ripened fruits or vegetables that were previously infested, and then brought into the home, or from fruit over-ripening in the home. Since adults can also fly from the outside through screened doors or windows, it can not always be assumed that the product in question was infested before it was brought into the home. The larvae are found on the inside layer of the fruit, directly beneath the skin. If the outer layer of the fruit is removed, the rest of the fruit can be salvaged. Fruit flies are primarily a nuisance pest.

FDA regulations

Defect action levels have been a part of the food industry for nearly a century. The first established defect action level was created in 1911 for mold in tomato pulp. However, limits for insect fragments and larvae were not added until the 1920s on various fruits and vegetables. In 1938, the Federal Food, Drug and Cosmetic Act (http://www.fda.gov/opacom/laws/fdcact/fdctoc.htm) was established to provide a more defined reference based on strict limitations and methods.[12]

Major companies spend a large amount of money every year to aid in the prevention of food contamination. Most of these dollars are well-spent and do, in fact, prevent food from becoming contaminated on a large scale; however, many "defects" are found in consumers' meals on a daily basis. The Food and Drug Administration states, “it is economically impractical to grow, harvest, or process raw products that are totally free of nonhazardous, naturally occurring, unavoidable defects”.[13]

The general public proposes that companies should use more chemicals or pesticides to control this “problem”, though the amount of pesticide and chemicals necessary to eradicate all insects from foodstuff would pose a threat to any human’s health, much more harmful than a controlled quantity of insect and rodent fragments. The food defect action levels, as proposed by the FDA, is a list of ordinances and guidelines by which manufacturers and industrial food agencies must abide to ensure the safe service of foodstuff. However, these detection levels are labeled with maximum limitations only. Due to the impossibility of preventing all unavoidable defects in foods, the FDA attempts to prevent these health hazards from reaching a harmful level. Therefore, it is understood and regarded that all manufactures are allowed to have low numbers of insect and rodent hairs present in food, as long as the product is still considered “safe” for human consumption.

Prevention and eradication

Prevention

To prevent the infestation of foodstuffs by pests of stored products, or “pantry pests”, a thorough inspection must be conducted of the food item intended for purchase at the supermarket or the place of purchase. The expiration date of grains and flour must also be noted, as products that sit undisturbed on the shelf for an extended period of time are more likely to become infested. This does not, however, exclude even the freshest of products from being contaminated. Packaging should be inspected for tiny holes that indicate there might be an infestation. If there is evidence of an insect infestation, the product should not be purchased. The store should be notified immediately, as further infestation must be prevented. Most stores have a plan of action for insect infestations. Bringing an infested product into a pantry or a home leads to a greater degree of infestation. In the home, putting cereal or grain-type items in protective containers will also help to prevent an infestation or the spread of insects from one product to another. Insects can chew through thin plastic, foil, cardboard and other packaging used for product for resale; transferring purchased products into heavy glass containers that can be tightly sealed or heavy plastic containers can improve sanitation and prevent infestation. Using the oldest products first and buying grains and cereals in smaller quantities which can be used quickly, depending on the size or intake of the family, decreases the chances of infestation. Fruit flies, however, present an entirely different approach to prevention. The primary method to controlling and eliminating fruit flies is to eradicate sources of attraction. Ripened produce should be either eaten, discarded, or refrigerated. Any damaged or cracked fruit or vegetable needs to be trimmed, and the damaged piece discarded in case larvae or eggs are present in the area in question. Careful attention must be paid to potential breeding sites that, when forgotten, could cause a massive infestation- all recycling and compost bins must be cleaned, and areas must be checked for forgotten, rotting fruit. Because of their small size, fruit flies are capable of breeding on the inside of the lid of a container. Therefore, when personally canning fruits or vegetables, beer, cider, or wine, the container must be well-sealed. Adults moths can lay eggs under the lid of a jar, allowing the larvae to crawl into the food source when hatched. Homeowners should also outfit their doors and windows with tight mesh screens to prevent the adult fruit flies from flying in from outdoors. Preventive methods and sanitation are the keys to avoiding an infestation or contamination of foodstuffs.[14][15]

Eradication

Although not seen when groceries are purchased, some products have the possibility of being infested prior to being placed in the pantry. A periodic check of susceptible foodstuffs is necessary, especially in summer months when most insects are more active. In the event an infestation is discovered, steps must be taken to eradicate the insects. Controlling an infestation is a lengthy process and insects may still be seen, albeit in dwindling numbers, for several weeks. All infested items, as well as uninfested

items, must be removed from shelves, thoroughly cleaned and vacuumed. After vacuuming, the waste containing the infested material must be removed and discarded. Items should be checked for beetles, larvae, and pupae; all food items must be inspected, as well, and special attention must be paid to items rarely used. The infested items may either be discarded, heated, or frozen to kill the insects. If the food is chosen to be discarded, the item must be completely removed from surrounding premises to prevent reinfestation. Freezing products for three to four days or heating them to about 130 to 140 °F for 30 to 40 minutes will rid the product of the pests. Decorative ornaments and objects made with plant material and seed in the vicinity of stored products will increase the risk of reinfestation; insects can feed on those items until they locate stored products. These items should also be thrown out or disinfected by freezing or heating. Cleaning the area where the infested products were found is advisable, as well. Cleaning with bleach or ammonia, however, will not help with the eradication of the pests. Using a vacuum cleaner to clean the area thoroughly, especially in cracks and corners where insects may hide, will decrease the chances of reinfestation. Because food will be stored in that area again, pesticides are not a good method of eradication. Pesticides can leave a residue that can contaminate food products stored near it. Also, once a pest is inside the container, the pesticides have no effect. If the infestation is so severe that pesticides are the only way to contain the problem, a professional should be contacted immediately. Do not try to apply pesticides to any area where food is stored for human or animal consumption. Contamination can occur and cause illness or more severe conditions. Proper storage and cleanliness are the only ways to prevent an infestation from occurring. Sanitation is the key to prevention and eradication of any pests.[14] [15]

Conclusion

If these insects are found infesting stored products, it is not practical to automatically assume the store or producer is at fault. Although some infestations are not the consumer's fault, producers are held by the FDA action defect levels to ensure their product does not contain more than the allotted amount of insects, insect fragments, or larvae. If a stored product is found to be infested by insects, and it is suspected that someone other than the consumer is at fault, a forensic entomologist can be contacted to make a determination. Again, it should not be assumed that these are the only five insects found in a common household pantry, but due to the large number of infestations by these five major groups, it can be safely deduced that it is perhaps one of these five. Stored product entomology is an important forensic field that is important to not only the government and the FDA but the general public, as it is involved in the consumption of food in everyday life.

Other stored product pests:

- Flour mite *Acarus siro*
- House cricket *Acheta domesticus*
- Common furniture beetle *Anobium punctatum*
- Varied carpet beetle *Anthrenus verbasci*
- Fur beetle or carpet beetle *Attagenus pellio*
- Black carpet beetle *Attagenus unicolor*
- Black larder beetle *Dermestes ater*
- Larder beetle *Dermestes lardarius*
- Hide beetle *Dermestes maculatus*
- Cacao moth *Ephestia elutella*
- Mediterranean flour moth *Ephestia kuehniella*
- Cigarette beetle *Lasioderma serricorne*
- Silverfish *Lepisma saccharina*
- Spider beetle *Mezium americanum*
- Red-legged ham beetle *Necrobia rufipes*
- Golden spider beetle *Niptus hololeucus*
- Yellow V moth *Oinophila v-flavum*
- Merchant grain beetle *Oryzaephilus mercator*
- Indian mealmoth *Plodia interpunctella*
- Australian spider beetle *Ptinus tectus*

- Meal moth *Pyralis farinalis*
- Lesser grain borer *Rhyzopertha dominica*
- Rice weevil *Sitophilus oryzae*
- Maize weevil *Sitophilus zeamais*
- Angoumois grain moth *Sitotroga cerealella*
- Drugstore beetle *Stegobium paniceum*
- Yellow mealworm *Tenebrio molitor*
- Cadelle beetle *Tenebroides mauritanicus*
- Red flour beetle *Tribolium castaneum*
- Confused flour beetle *Tribolium confusum*
- Destructive flour beetle *Tribolium destructor*
- Carpet moth or tapestry moth *Trichophaga tapetzella*
- Khapra beetle *Trogoderma granarium*
- Clothes moths – several species

See also

- List of common household pests
- The Food Defect Action Levels

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Further reading

- Robinson, W. H. (2008). *Urban Insects and Arachnids A Handbook of Urban Entomology*. Cambridge University Press. ISBN 978-0-521-81253-5, ISBN 0-521-81253-4. Also available in eBook format.

External links

- Indianmeal moth, *Plodia interpunctella* (http://entomology.ifas.ufl.edu/creatures/urban/stored/indianmeal_moth.htm) on the University of Florida/IFAS Featured Creatures Web site
- red and confused flour beetles, Tribolium *spp.* (http://entomology.ifas.ufl.edu/creatures/urban/beetles/red_flour_beetle.htm) *on the UF/IFAS Featured Creatures Web site*
- a stored product pest, *Oryzaephilus acuminatus* (http://entomology.ifas.ufl.edu/creatures/urban/stored/o_acuminatus.htm) on the UF/IFAS Featured Creatures Web site
- FAO (http://www.fao.org/DOCREP/003/T0146E/T0146E02.htm) Insect pests of cured fish
- PADIL (https://web.archive.org/web/20080805231925/http://www.padil.gov.au/browsePestRegions.aspx?menu=p2&group=1&o=1&id=6&paging=No) Long download.

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Flour mite

The **flour mite**, ***Acarus siro***, (Hindi - घुन, *Ghun*) a pest of stored grains,[1][2] is one of many species of grain and flour mites.[3] An older name for the species is *Tyroglyphus farinae*.[4]

The flour mite, which is pale greyish white in colour with pink legs, is the most common species of mite in foodstuffs. The males are from 0.33–0.43 millimetres (0.013–0.017 in) long and the female is from 0.36–0.66 mm (0.014–0.026 in) long.

Flour mites contaminate grain and flour by allergens and they transfer pathogenic microorganisms. Foodstuffs acquire a sickly sweet smell and an unpalatable taste. When fed infested feeds, animals show reduced feed intake, diarrhea, inflammation of the small intestine, and impaired growth. Pigs have their live-weight gain, feed-to-gain ratio, and nitrogen retention markedly reduced by infested feeds.

Flour mites are intentionally inoculated into Mimolette cheese to improve the flavor.[5] When used for this purpose, they may be referred to as "cheese mites".

The mites sometimes bite humans, which can cause an allergic reaction known as Baker's itch.[6][7]

Flour mite	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Arachnida
Subclass:	Acari
Order:	Sarcoptiformes
Family:	Acaridae
Genus:	*Acarus*
Species:	***A. siro***
Binomial name	
Acarus siro Linnaeus, 1758	

See also

- List of mites associated with cutaneous reactions

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External links

- Wikihow (https://www.wikihow.com/Get-Rid-of-and-Prevent-Flour-Mites) How to Get Rid of and Prevent Flour Mites (domestic infestations)

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House cricket

Acheta domesticus, commonly called the **house cricket**, is a cricket most likely native to Southwestern Asia, but between 1950 and 2000 it became the standard feeder insect for the pet and research industries and spread worldwide.[2][3] but can be kept as pets themselves, as this has been the case in China and Japan.[4]

House cricket

Scientific classification
Kingdom: Animalia
Phylum: Arthropoda
Class: Insecta
Order: Orthoptera
Suborder: Ensifera
Family: Gryllidae
Genus: *Acheta*
Species: ***A. domesticus***
Binomial name
Acheta domesticus (Linnaeus, 1758) [1]

Contents

Description

Life cycle

Diseases

Human consumption

Nutrition

References

External links

Description

The house cricket is typically gray or brownish in color, growing to 16–21 millimetres (0.63–0.83 in) in length. Males and females look similar, but females will have an ovipositor emerging from the rear, around 12 millimetres (0.47 in) long. The ovipositor is brown-black, and is surrounded by two appendages. On males, the cerci are also more prominent.[5]

Life cycle

House crickets take two to three months to complete their life cycle at 26 to 32 °C (79 to 90 °F). They have no special overwintering stage, but can survive cold weather in and around buildings, and in dumps where heat from fermentation may sustain them. Eggs are deposited in whatever damp substrate is available. Juveniles resemble the adults except for being smaller and wingless.[2]

Diseases

The house cricket was essentially eliminated from the cricket-breeding industries of North America and Europe by the appearance of cricket paralysis virus which spread rapidly in Europe in 2002 and then in the United states in 2010. The virus is extremely lethal to this species of cricket and a few others, and left many hobbyists and researchers without adequate feeder insects. It has been replaced by the Jamaican field cricket, which is resistant to cricket paralysis virus and has many of the desirable features of the house cricket.[6]

Human consumption

The house cricket is an edible insect. It is farmed in South-East Asia and parts of Europe and North America for human consumption. In Asia it is said to become more popular than many native cricket species due to what consumers claimed was their superior taste and texture.[7] Dry-roasting is common and is considered the most nutritious method of preparing them, though they are often sold deep-fried as well.[8][9] Farmed house crickets are mostly freeze-dried and often processed into a powder known as cricket flour.[10] In Europe, the house cricket is officially approved for use in food products in Switzerland (since 2017).[11]



Deep-fried house crickets sold as food at a market in Thailand

Nutrition

Like all insects, crickets are a complete protein. They contain both omega-3 and omega-6 fatty acids.[12]

Nutrition Information[13][14][15][16]

Serving size: 1 1/2 cup (30g)		
Quantity per Serving		
Calories	150	
Total Fat	6	g
Saturated fat	2.3	g
Trans fat	0.05	g
Cholesterol	50	mg
Sodium	100	mg
Total Carbohydrate	6	g
Dietary Fiber	6	g
Protein	18	g
Vitamin D	0.22	
Vitamin B12	0.86	µg
Calcium	38.5	mg
Iron	1.6	mg
Potassium	273	mg

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External links

Media related to House cricket at Wikimedia Commons

- Sound recordings of *Achetus domesticus* at BioAcoustica (http://bio.acousti.ca/taxonomy/term/92)

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Common furniture beetle

The **common furniture beetle** or **common house borer** (*Anobium punctatum*) is a woodboring beetle. In the larval stage it bores in wood and feeds upon it. Adult *Anobium punctatum* measure 2.7–4.5 millimetres (0.11–0.18 in) in length. They have brown ellipsoidal bodies with a prothorax resembling a monk's cowl .[1]

Common furniture beetle	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Ptinidae
Genus:	*Anobium*
Species:	***A. punctatum***
Binomial name	
Anobium punctatum De Geer, 1774	

Contents

Life cycle

Pest control

See also

References

Life cycle

Adults do not feed; they just reproduce. The female lays her eggs in cracks in wood or inside old exit holes, if available. The eggs hatch after some three weeks, each producing a 1 millimetre (0.039 in) long, creamy white, C-shaped larva. For three to four years the larvae bore semi-randomly through timber, following and eating the starchy part of the wood grain, and grow up to 7 millimetres (0.28 in). They come nearer to the wood surface when ready to pupate. They excavate small spaces just under the wood surface and take up to eight weeks to pupate. The adults then break through the surface, making a 1 mm to 1.5 millimetres (0.059 in) exit hole and spilling dust, the first visible signs of an infestation.

Pest control

The first step in pest control is prevention. Particularly important in this respect is to keep the timber dry - below 16% moisture content. A relative humidity within the building above 60% may lead to an infestation, and timber moisture content below 12% is too dry for an infection to occur.[2] *Anobium punctatum* normally only attacks seasoned sapwood timber, not live or fresh wood. Also, it usually does not attack heartwood timbers. This is readily observed from infested structures, where one piece of timber may be heavily attacked but an adjacent one left virtually untouched according to whether it is made from the heartwood or the sapwood part of a tree trunk. Infestations are also usually a problem of old wooden houses built with untreated timbers. Some building regulations state that timbers with more than 25% sapwood may not be used, so that wood borer infections can not substantially weaken structures.



Woodworm holes and burrows exposed in wooden floorboard

Infection, past or present, is diagnosed by small round exit holes of 1 to 1.5 mm diameter. Active infections feature the appearance of new exit holes and fine wood dust around the holes.

Because of the 3–4 year life cycle of *Anobium punctatum*, timber or timber products bought containing an *A. punctatum* infection may not manifest holes until years after the timber has been acquired. Infestation can be controlled by application of a residual insecticide (such as permethrin) to infected areas, by professional fumigation, or by replacing infected timber .[3] Simple aerosol insecticide sprays will only kill the adult borer on the wing but not the burrowing larvae, which remain relatively protected inside infected timbers. Freezing infected timber, or heating to 50 °C for a day or more, will kill beetle larvae, but offer no residual protection.

See also

- Woodworm

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Varied carpet beetle

The **varied carpet beetle** (*Anthrenus verbasci*) is a 3 mm-long beetle belonging to the family Dermestidae. They are a common species, often considered a pest of domestic houses and, particularly, natural history museums, where the larvae may damage natural fibers and can damage carpets, furniture, clothing, and insect collections. *A. verbasci* was also the first insect to be shown to have an annual behavioral rhythm[1] and to date remains a classic example of circannual cycles in animals.

Contents

Description
Life cycle
Distribution and habitat
Diet and behaviour
Predators
Interaction with humans
As a domestic pest
As a museum pest
References
External links

Description



Larval form of *Anthrenus verbasci* (4.6 mm long)

Adult *A. verbasci* range in length from 1.7 to 3.5 mm (0.07 to 0.14 in). The body is rounded, almost spherical. The elytra and pronotum are covered in fine scales of different colours, creating an irregular pattern of white, brownish and yellowish patches on these features. The white scales are focussed along the lateral margins of the pronotum and on the elytra, where they form three bright, wavy transverse bands. In addition to these morphological features, their antennae are 11-segmented, with a club of 3 segments.[2]

Varied carpet beetle



Dorsal view



Side view

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Dermestidae
Genus:	*Anthrenus*
Species:	***A. verbasci***

Binomial name

Anthrenus verbasci
(Linnaeus, 1767)

Synonyms

- *Anthrenus varius* Fabricius, 1775
- *Nathrenus verbasci*

The larval form of *A. verbasci*, commonly known as '**woolly bears**' (a name shared with the larvae of *Arctia caja* and many other moths of the subfamily Arctiinae), measures up to 4–5 millimetres (0.16–0.20 in) in length. The larvae are elongated and densely covered in large setae (hairs). These hairs are organised into alternating, transverse groups of light and dark-brown patches: the larva appears covered in brown stripes. The body is usually wider at the back than at the front where it also bears 3 pairs of hair tufts along its rear abdomen that can be used for self-defense.[3]

Life cycle

A. verbasci has a life cycle ranging from 1–3 years, depending upon the environmental conditions. A study in 1958 found that temperature is able to affect larval development, concluding that the periods of incubation and pupation of *A. verbasci* decrease with increase of temperature (the life cycle is thus quickened with a modern rise in temperature). Incubation decreased from 54 days at 15 °C to 12 days at 30 °C, and the pupation decreased from 89 days at 10 °C to 9 days at 25 °C. Relative humidity was shown to have little effect.[4]



Larva of *A. verbasci*. Front view

Larvae hatch from eggs in the spring and early summer, often in the nests of birds (including those of the house sparrow and house swift) or around stored fabrics.[5]

Adults emerge between late May and early August, flying to and feeding on the pollen and nectar of flowering plants.[6] The life expectancy of the beetle is about two weeks. During this period, mating occurs and the eggs are laid, either close to the human environs or in bird nests, tree hollows and similar, dry places where larvae can find their food. Then the cycle begins anew.

Distribution and habitat

This species is present in most of Europe, in the eastern Palearctic ecozone, in the Near East, in the Nearctic ecozone, in North Africa and in North Asia, also in the Neotropics.[7]

Diet and behaviour

Larvae feed on keratin and chitin of natural fibers (dead insects, animal hair and feathers) throughout their development, eventually experiencing a dormancy period (also known as diapause) prior to pupation into the adult stage. The length of the dormancy appears to depend on environmental factors, with the most likely zeitgeber being photoperiod.[5] Adults feed on the pollen and nectar of flowering plants.[6]

Predators

Among the natural predators of *A. verbasci*, one of the most well-studied is the parasitoid wasp *Laelius pedatus* (in the family Bethylidae).[8] Upon discovering an *A. verbasci* larva, a female wasp will land on the larva's dorsal side and attempt to line up its long, stinger-like ovipositor for a paralyzing blow to the thorax. In response, the larva will erect long hairs on their abdomen and attempt to brush these hairs against the encroaching wasp. The hairs detach and stick to the wasp on contact, presumably causing some sort of irritation. Evidently, such irritation is not enough to deter an attack on *A. verbasci* larvae, as the vast majority of attacks are successful. By comparison, the closely related beetle species *Anthrenus flavipes* – which has slightly longer hairs than *A. verbasci* – uses such a defense more effectively.[8]

After a single successful sting, the beetle is permanently paralyzed. The entire process from landing to complete paralysis lasts approximately 40 seconds.[8] *L. pedatus* does not lay eggs immediately after the beetle is paralyzed, waiting as long as 24 hours before oviposition. During this time, she grooms herself, removing any hairs that might have stuck to her during the attack.

During this lengthy process she appears to monitor the larva's state of paralysis by repeatedly biting it and monitoring its reaction. Once sufficiently clear of hairs, the wasp creates a bare patch on the larva's abdomen and lays 2–4 eggs. Eggs hatch in 3–4 days and the larvae feed on the beetle for 3–7 days, eventually killing the host. They then spin cocoons near the empty shell of the host, emerging some time later as adult wasps.[8]

Interaction with humans

As a domestic pest

The larvae of *A. verbasci* are a common household pest. Adult beetles usually lay their eggs in air ducts, in closets, under furniture, or under baseboards.[9] Once hatched and until they pupate into adults, the larvae hide in dark, undisturbed areas and feed on organic material. The larvae are thus responsible for the damage of various items, such as furniture, clothing, blankets, furs, and carpets. They are commonly found in musical instruments which have been stored for lengthy periods of time, feeding on pads and felts most commonly found in woodwind instruments.



Anthraenus verbasci caught on a sticky blunder trap in a museum.

As a museum pest

Collections of specimens, especially of insects, are also vulnerable to attack, making *A. verbasci* a common pest in museums.[10] In a 1987 survey of British national history museums, at least five noted that *A. verbasci* was categorised as a major pest for biological collections.[11] Larvae are often found in the nests of sparrows and wagtails,[12] and so larvae and adults may enter museums at upper levels through windows and roof spaces.[11]

Infestations can be prevented by removing the larvae and adults through regular vacuum cleaning, dry cleaning or airing clothing outside, placing naphthalene balls in closets, and removing abandoned bird and insect nests attached to the building.[9] Signs of an infestation include the presence of damaged articles, moulted larval skins in dark areas, and an abundance of adult beetles near windows.[9] Susceptible people may also find that hairs shed from the larvae cause irritated itchy welts that may be confused with bedbug bites.[13] Deterring or killing *A. verbasci* can be accomplished using insecticides,[9] oxygen deprivation,[14] freezing,[15] and pheromone[16] and scent traps.[16]

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- Fauna Europaea (http://www.faunaeur.org/full_results.php?id=413742)
- Invertebrate Ireland on line (http://www.gwydir.demon.co.uk/insects/dermestidae.htm#anthrenus)
- Dermestidae of the World (http://www.dermestidae.com/Anthrenusverbasci.html) Habitus, abdomen and antennae.
- Varied Carpet Beetle Fact Sheet (http://www.pestworld.org/pest-guide/other-pests/varied-carpet-beetles/)
- Varied Carpet Beetle Allergy and Treatment (http://insect-identification.com/carpet-beetle-allergy/)
- Museumpests.net - Varied Carpet Beetle Museum factsheet (http://museumpests.net/wp-content/uploads/2014/03/Varied-Carpet-Beetle.pdf)
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- **Wikispecies**

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Attagenus pellio

Attagenus pellio, the **fur beetle** or **carpet beetle**, is an important pest damaging stored products such as furs, skins, textiles and grain.

Attagenus pelio is a 4–6 mm-long oval shaped insect with two patches of white hair on the elytra.

See also

Home stored product entomology

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External links

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Carpet Beetle	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Dermestidae
Genus:	*Attagenus*
Species:	***A. pellio***
Binomial name	
Attagenus pellio (Linnaeus, 1758)	

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Dermestes ater

Dermestes ater, also occasionally called Dermestes haemorrhoidalis, is a species of beetle in the family Dermestidae, the skin beetles. It is known commonly as the **black larder beetle** or **incinerator beetle**.[1] It is native to North America, but today it is found nearly worldwide. Like several other dermestid beetles, this species is familiar as a common pest of stored products.[1]

Dermestes ater	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Dermestidae
Genus:	*Dermestes*
Species:	***D. ater***
Binomial name	
Dermestes ater De Geer, 1774	

Contents

Description
Life cycle
Economic and scientific importance
References

Description

The adult beetle is about 7 to 9 millimeters long. It has black or brown elytra and a coating of yellowish hairs. The male can be distinguished from the female by a row of bristles along the abdomen. The larva is white with long dark bristles, its body darkening in color to black, brown, or reddish as it grows. It reaches a maximum length around 14 millimeters.

Life cycle

The female lays 1 to 25 eggs at a time. They are whitish and about 2 millimeters long. The eggs hatch in a few days, depending on temperature. Larval development also depends on temperature, as well as humidity and food availability. Each larva may proceed through six to nine instars, taking 19 to 50 days to grow to maximum size. It then pupates for several days. The adult lives for around 169 days, depending on temperature.[1]

Economic and scientific importance

The beetle attacks many types of stored food and other products. It has been found in cheese, dried fish, leather, copra, silk, wool, milk powder, incinerated waste,[1] hog bristles, dried mushrooms, cacao, and ginger.[2]

It is an occasional predator, feeding on live insects; it is a pest of the sericulture industry because it preys on silkworm pupae, damaging the silk cocoons in the process.[3] It also feeds on housefly (*Musca domestica*) larvae and pupae in places where both insects congregate, such as poultry houses.[4] The adult may cannibalize larvae and pupae of its own species, and the larvae may eat each other and the eggs.[1] It is also a scavenger of dead animals.[2] It is a pest of museum collections, such as dried insects.[1] It has been found living in and consuming human corpses, so it may play a role in forensic entomology.[5]

The beetle carries several parasites including chicken tapeworms, and are found inhabiting chicken coops where they can spread the parasites to the birds.[6]

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Ephestia elutella



Caterpillars

Ephestia elutella, the **cacao moth**, **tobacco moth** or **warehouse moth**, is a small moth of the family Pyralidae. It is probably native to Europe, but has been transported widely, even to Australia. A subspecies is *E. e. pterogrisella*.

The wingspan is 14–20 mm. This moth flies throughout the warmer months, e.g. from the end of April to October in Belgium and the Netherlands.

The caterpillars are often considered a pest, as they feed on dry plant produce, such as cocoa beans and tobacco, as well as cereals and dried fruit and nuts. Less usual foods include[1] dried-out meat and animal carcasses, specimens in insect collections, and dry wood.

This species has been known under a number of junior synonyms:[2]

- *Ephestia amarella* Dyar, 1904
- *Ephestia icosiella* Ragonot, 1888
- *Ephestia infumatella* Ragonot, 1887
- *Ephestia roxburghi* (*lapsus*)
- *Ephestia roxburghii* Gregson, 1873
- *Ephestia roxburgii* (*lapsus*)
- *Ephestia uniformata* Dufrane, 1942 (variety)
- *Homoeosoma affusella* Ragonot, 1888
- *Hyphantidium sericarium* Scott, 1859
- *Phycis angusta* (Haworth, 1811)
- *Phycis elutea* Haworth, 1811; (unjustified emendation)
- *Phycis rufa* Haworth, 1811
- *Phycis semirufa* Haworth, 1811
- *Tinea elutella* Hübner, 1796

Cacao moth	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
Family:	Pyralidae
Tribe:	Phycitini
Genus:	*Ephestia*
Species:	***E. elutella***
Binomial name	
Ephestia elutella (Hübner, 1796)	
Synonyms	
Numerous, see text	

Footnotes

1. Grabe (1942)
2. See references in Savela (2009)

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External links

- Lepidoptera of Belgium (http://webh01.ua.ac.be/vve/Checklists/Lepidoptera/Pyralidae/Eelutella.htm)
- Cacao moth on UKMoths (https://ukmoths.org.uk/show.php?id=3328)

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Silverfish

A **silverfish** (*Lepisma saccharina*) is a small, wingless insect in the order Zygentoma (formerly Thysanura). Its common name derives from the animal's silvery light grey colour, combined with the fish-like appearance of its movements. However, the scientific name (*L. saccharina*) indicates the silverfish's diet consists of carbohydrates such as sugar or starches.

Contents

Description
Distribution
Reproduction and life cycle
Ecology
Etymology
Evolution
Similar species
References
External links

Lepisma saccharina

Temporal range: 400–0 Ma

Pre Є Є O S D C P T J K Pg N

Emsian to Recent[1]



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Hexapoda
Class:	Insect
Subclass:	Apterygota
Order:	Zygentoma
Family:	Lepismatidae
Genus:	*Lepisma*
Species:	***L. saccharina***

Binomial name

Lepisma saccharina

Linnaeus, 1758

Description

Silverfish are nocturnal insects typically 13–25 mm (0.5–1.0 in) long.[2] Their abdomens taper at the end, giving them a fish-like appearance.[3] The newly hatched are whitish, but develop a greyish hue and metallic shine as they get older.[4] They have two long cerci and one terminal filament at the tip of the abdomen between the cerci. They also have two small compound eyes, despite other members of Zygentoma being completely eyeless, such as the family Nicoletiidae.[3][5]

Like other species in Apterygota, silverfish are completely wingless.[3][6] They have long antennae, and move in a wiggling motion that resembles the movement of a fish.[7] This, coupled with their appearance and silvery scales, inspires their common name. Silverfish typically live for two to eight years.[4] Silverfish are agile runners and can outrun most of their predators (including wandering spiders and centipedes). However, such running is possible only on horizontal surfaces, as they lack any additional appendages, and therefore are not fast enough to climb walls at the same speed. They also avoid light.[8]

Distribution

Silverfish are a cosmopolitan species, found in Africa, the Americas, Australia, Eurasia, and other parts of the Pacific.[9] They inhabit moist areas, requiring a relative humidity between 75% and 95%.[10] In urban areas, they can be found in attics, basements, bathtubs, sinks, kitchens, old books, classrooms, and showers.[4]

Reproduction and life cycle



A silverfish

Before silverfish reproduce, they carry out a ritual involving three phases, which may last over half an hour. In the first phase, the male and female stand face to face, their quivering antennae touching, then repeatedly back off and return to this position. In the second phase, the male runs away and the female chases him. In the third phase, the male and female stand side by side and head to tail, with the male vibrating his tail against the female.[11] Finally, the male lays a spermatophore, a sperm capsule covered in gossamer, which the female takes into her body via her ovipositor to fertilize her eggs. The female lays groups of fewer than 60 eggs at once, deposited in small crevices.[12] The eggs are oval-shaped, whitish, about 0.8 mm (0.031 in) long,[13] and take between two weeks and two months to hatch. A silverfish usually lays fewer than 100 eggs in her lifetime.[2]

When the nymphs hatch, they are whitish in colour, and look like smaller adults. As they moult, young silverfish develop a greyish appearance and a metallic shine, eventually becoming adults after three months to three years.[12] They may go through 17 to 66 moults in their lifetimes, sometimes 30 in a single year—many more than most insects. Silverfish are among the few types of insect that continue to moult after reaching adulthood.[14]

Ecology

Silverfish consume matter that contains polysaccharides, such as starches and dextrin in adhesives.[4] These include book bindings, carpet, clothing, coffee, dandruff, glue, hair, some paints, paper, photos, plaster, and sugar. They will damage wallpaper in order to consume the paste.[15] Silverfish can also cause damage to tapestries. Other substances they may eat include cotton, dead insects, linen, silk, leftover crumbs, or even their own exuvia (moulted exoskeleton). During famine, a silverfish may even consume leatherware and synthetic fabrics. Silverfish can live for a year or more without eating if water is available.[2][4][16]



Pages in a book damaged by silverfish that consumed portions of it.

Silverfish are considered household pests, due to their consumption and destruction of property.[2] However, although they are responsible for the contamination of food and other types of damage, they do not transmit disease.[4][17] Earwigs, house centipedes, and spiders are known to be predators of silverfish.[18][19]

Etymology

The scientific name for the species is *Lepisma saccharina*, due to its tendency to eat starchy foods high in carbohydrates and protein, such as dextrin.[4] However, the insect's more common name comes from its distinctive metallic appearance and fish-like shape.[20] While the scientific name can be traced back to 1758, the common name has been in use since at least 1855.[21][22]

Evolution

Together with jumping bristletails, the predecessors of silverfish are considered the earliest, most primitive insects. They evolved at the latest in mid-Devonian and possibly as early as late Silurian more than 400 million years ago.[1] Some fossilized arthropod trackways from the Paleozoic Era, known as *Stiaria intermedia* and often attributed to jumping bristletails, may have been produced by silverfish.[23]

Similar species



Ctenolepisma species

Other similar insect species are also known as silverfish. Two other silverfish are common in North America, *Ctenolepisma longicaudata* and *Ctenolepisma quadriseriata*.[12] *Ctenolepisma urbana* is known as the urban silverfish.[9] The Australian species most commonly referred to as silverfish is a different lepismatid, *Acrotelsella devriesiana*.[3] The firebrat (*Thermobia domestica*) is like a silverfish, but with a mottled gray and brown body.[24]

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External links

- Fact sheet on silverfish highlighting habits, habitat and threats (http://www.pestworld.org/pest-guide/occasional-invaders/silverfish/)
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Mealworm

Mealworms are the larval form of the **mealworm beetle**, *Tenebrio molitor*, a species of darkling beetle. Like all holometabolic insects, they go through four life stages: egg, larva, pupa, and adult. Larvae typically measure about 2.5 cm or more, whereas adults are generally between 1.25 and 1.8 cm in length.

Mealworm beetle

Temporal range: Holocene, 0.003–0 Ma

Pre Є Є O S D C P T J K PgN



Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Tenebrionidae
Genus:	*Tenebrio*
Species:	***T. molitor***

Binomial name

Tenebrio molitor

Linnaeus, 1758

Contents

Reproduction
- Sex pheromones

Relationship with humans
- As pests
- As food
 - Nutrient composition
- In waste disposal

See also

Gallery

References

External links

Reproduction

The mealworm beetle breeds prolifically. Mating is a three-step process: the male chasing the female, mounting her and inserting his aedeagus, and injecting a sperm packet. Within a few days the female burrows into soft ground and lays about 500 eggs.

After four to 19 days the eggs hatch. Many predators target the eggs, including reptiles.

During the larval stage, the mealworm feeds on vegetation and dead insects and molts between each larval stage, or instar (9 to 20 instars). After the final molt it becomes a pupa. The new pupa is whitish, and it turns brown over time. After 3 to 30 days, depending on environmental conditions such as temperature, it emerges as an adult beetle.

Sex pheromones

A sex pheromone released by male mealworms has been identified.[1] Inbreeding reduces the attractiveness of sexual pheromone signaling by male mealworms.[2] Females are more attracted to the odors produced by outbred males than the odors produced by inbred males. The reduction of male signaling capability may be due to increased expression of homozygous deleterious recessive

alleles caused by inbreeding.[3]

Relationship with humans

Tenebrio molitor is often used for biological research. Its relatively large size, ease of rearing and handling, and status as a non-model organism make it useful in proof of concept studies in the fields of basic biology, biochemistry, evolution, immunology and physiology.



Mealworms (larvae of *Tenebrio molitor*) illustrated by Des Helmore

As pests

Mealworms have generally been considered pests, because their larvae feed on stored grains. Mealworms probably originated in the Mediterranean region, but are now present in many areas of the world as a result of human trade and colonization. The oldest archaeological records of mealworms can be traced to Bronze Age Turkey. Records from the British Isles and northern Europe are from a later date, and mealworms are conspicuously absent from archaeological finds from ancient Egypt.[4]

As food

Mealworms are edible for humans, and are commonly consumed in a practice known as entomophagy. Mealworms have historically been consumed in many Asian countries, particularly in Southeast Asia. They are commonly found in food markets and sold as street food alongside other edible insects. Baked or fried mealworms have been marketed as a healthy snack food in recent history, though the consumption of mealworms goes back centuries. They may be easily reared on fresh oats, wheat bran or grain, with sliced potato, carrots, or apple as a moisture source. The small amount of space required to raise mealworms has made them popular in many parts of Southeast Asia.

Mealworms have been incorporated into tequila-flavored novelty candies. Mealworms are not traditionally served in tequila, and the "tequila worm" in certain mezcals is usually the larva of the moth *Hypopta agavis*.

Mealworms are typically used as a pet food for captive reptiles, fish, and birds. They are also provided to wild birds in bird feeders, particularly during the nesting season. Mealworms are useful for their high protein content. They are also used as fishing bait.

They are commercially available in bulk and are typically available in containers with bran or oatmeal for food. Commercial growers incorporate a juvenile hormone into the feeding process to keep the mealworm in the larval stage and achieve an abnormal length of 2 cm or greater.[5]

Nutrient composition

Mealworm larvae contain significant nutrient content, a feature that has made them viable as food and feed. For every 100 grams of raw mealworm larvae, 206 calories and anywhere from 14 to 25 grams of protein are contained.[6] Mealworm larvae contain levels of potassium, copper, sodium, selenium, iron and zinc that rival that of beef. Mealworms contain essential linoleic acids as well. They also have greater vitamin content by weight compared to beef, B12 not included.[6][7]

In waste disposal

In 2015, it was discovered that mealworms can degrade polystyrene into usable organic matter at a rate of about 34-39 milligrams per day. Additionally, no difference was found between mealworms fed only styrofoam and mealworms fed conventional foods, during the one-month duration of the experiment.[8] Microorganisms inside the mealworm's gut are responsible for degrading the polystyrene, with mealworms given the antibiotic gentamicin showing no signs of degradation.[9] Isolated colonies of the mealworm's gut microbes, however, have proven less efficient at degradation than the bacteria within the gut.[9] No attempts to commercialize this discovery have been made.[*citation needed*]

See also

- Zond 5, a 1968 space mission on which mealworms were among the first earthlings to fly to the Moon

Gallery



In a bedding of bran



In a bowl



Mealworm detail



A mealworm pupa with molted larval skin



New adult



Mature adult

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External links

- Darkling Beetle/Mealworm Information. (https://web.archive.org/web/20040603084901/http://insected.arizona.edu/mealinfo.htm) Center for Insect Science Education Outreach. University of Arizona.
- Mealworms and Darkling Beetles (*Tenebrio* beetle). (http://lhsfoss.org/fossweb/teachers/materials/plantanimal/tenebriobeetles.html) FOSSweb.
- Mealworms.org (http://mealworms.org/)
- How to Raise Mealworms (https://atbuz.com/post/raise-mealworms/)
- How to Care for Mealworms (https://atbuz.com/post/care-for-mealworms/)

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Pyralis farinalis

"Meal moth" redirects here; not to be confused with "flour moth (disambiguation)".

Pyralis farinalis, the **meal moth**, is a cosmopolitan moth of the family Pyralidae. Its larvae (caterpillars) are pests of certain stored foods, namely milled plant products.

It is the type species of the genus *Pyralis*, and by extension of its entire tribe (Pyralini), subfamily (Pyralinae) and family. Its synanthropic habits were noted even by 18th- and 19th-century naturalists, who described it using terms like *domesticalis* ("of home and hearth"), *fraterna* ("as close as a brother"), or the currently-valid *farinalis* ("of the flour").[1]

At rest, adult moths (imagines) typically hold the tip of their abdomen at 90° to their body. Their upperwings are fairly colourful by moth standards, and have a wingspan of 18–30 mm. Adults fly from June to August.[2] Adults do not live long after mating and eggs hatch quickly, which leads this moth to have a quick life cycle and be able to produce multiple generations within a single year.

In Great Britain and some other locations – particularly outside its natural range – it is mostly restricted to anthropogenic habitats of stored grain, e.g. barns and warehouses. However, it has been found in almond orchards among plant detritus and poultry farms among chicken manure.

P. farinalis is a species that is well adapted to living among humans and the urbanization that comes along with them. Though considered a pest to most since it can decimate grain storages, humans have found a use for this pesky moth. In Chinese culture it is the main ingredient of "insect tea." This drink is popular enough that scientists have been studying the moth's optimum growth conditions so they can possibly cultivate it for commercial use.[3]

Meal moth



Adult from above



The underwings have no conspicuous pattern

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
Family:	Pyralidae
Genus:	*Pyralis*
Species:	***P. farinalis***

Binomial name

Pyralis farinalis
(Linnaeus, 1758)

Contents

Geographic range

Habitat

Food resources
- Caterpillar

Life history
- Life cycle
 - Egg
 - Caterpillar
 - Pupae
 - Adult

Enemies
Parasites
Mating
Female/male interactions
Pheromones
Interactions with humans
Pest of crop plants
Agricultural use
Footnotes
References

Geographic range

Pyralis farinalis has been described as a "cosmopolitan" species, which means its range extends across most of the world.[4] It is found all across the United States, but is mostly found along the eastern coast. This moth is most commonly seen in the Northeastern region.[5] It is also found in Great Britain in the Falkland Islands and in China.[6][4]

Habitat

P. farinalis is typically found in silos or other grain storage buildings where the grain is stored poorly and moisture is able to infiltrate the grain supply. Places where refuse vegetable matter is able to accumulate are more likely to house *P. farinalis* than grain storage buildings where the environment is clean and dry.[7] *P. farinalis* prefers to live in detritus and has been found in non-urban areas in almond orchards.[8] Meal moths can live in various habitats of damp, moist plant debris, but also even in poultry manure.[4]

Food resources

Caterpillar

As caterpillars, *P. farinalis* subsists mostly on cereals, but will also feed upon other types of grain and vegetables, such as potatoes. The meal moth's larvae are also interesting because they feed on all parts of the grain plant and do not seem to have any preference for one part of another. The larvae are equally likely to eat a cereal plant's seed, bran, husk, or straw.[7]

Life history

Originally thought to be biennial species, it has been found that *P. farinalis* typically completes its entire life cycle in the course of eight weeks, and is capable of producing four generations within a year.[7] Fast life cycles in these moths allow them to reproduce and grow their populations rapidly.[4]

Life cycle

Egg

The eggs of *P. farinalis* are ellipsoid in shape and very wrinkled with creases running lengthwise along the egg.[9] These wrinkles form a reticulated pattern on the surface of the egg.[4] Eggs are usually laid between two and five days after copulation and hatch after a nine-day incubation period.[10][4] Healthy females produce an average of 235 eggs in her lifetime.[10]

Caterpillar

The larvae of *P. farinalis* spend most of their time out of sight of predators and humans. They live in tunnels of silk and meal particles which keep them safe from predators and they come to the openings of these tunnels to feed.[4]

Pupae

Once fully grown, the caterpillars leave their tubes and spin a cocoon where they will develop into an adult. After 6–8 weeks the pupae will emerge as fully developed adults.[4]

Adult

Adults were usually fully developed between 60–65 days after oviposition. Virgin adults would then mate as quickly as possible. Once mated, males and females would usually only live for nine to ten more days.[4]

Enemies

Parasites

P. farinalis is parasitized by a number of species. These include:[11]

- *Meteorus ictericus*
- *Tetrasticus*
- *Lespidea tarsalis*
- *Apantales carpatus*
- *Goniozus columbianus*
- *Metacoelus mansuetos*
- *Melanophora roralis*

Mating

Female/male interactions

Pheromones

An odd behavior that male meal moths exhibit is the attempt to mate with other species, such as *Amyelois transitella*. It is hypothesized that these two species share the sex pheromone (Z,Z)-11,13-hexa decadienal which female *A. transitella* use to attract males of their species. However, male *P. farinalis* are also attracted to this pheromone and will court and copulate with *A. transitella* females, but it is unlikely that offspring of these copulations would be viable.[8]

Interactions with humans

Pest of crop plants

Because of the meal moth's extensive appetite for cereals and grains, it is considered a pest by agriculturists. If grain is not stored properly, then a colony of meal moths can do considerable damage to the crop.[7][4]

Agricultural use

One of the most surprising uses for *P. farinalis* is its use in producing "insect tea" in China. In China, the moth lives on the host plant of *Litsea coreana* and scientists have been studying optimum temperatures for which the moth is able to grow and develop best in the hopes of being able to cultivate the moths for insect tea.[3]

Footnotes

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Economic entomology

Economic entomology is a field of entomology, which involves the study of insects that benefit or harm humans, domestic animals, and crops. Insects that cause losses are termed as pests. Some species can cause indirect damage by spreading diseases and these are termed as vectors. Those that are beneficial include those reared for food such as honey, substances such as lac or pigments and for their role in pollinating crops and controlling pests.

The *Journal of Economic Entomology*, published by the Entomological Society of America, described itself in 2017 as the "most-cited entomological journal".[1]

Contents

History
- 19th century
- 20th century

Harmful insects

Beneficial insects

References

Further reading

History

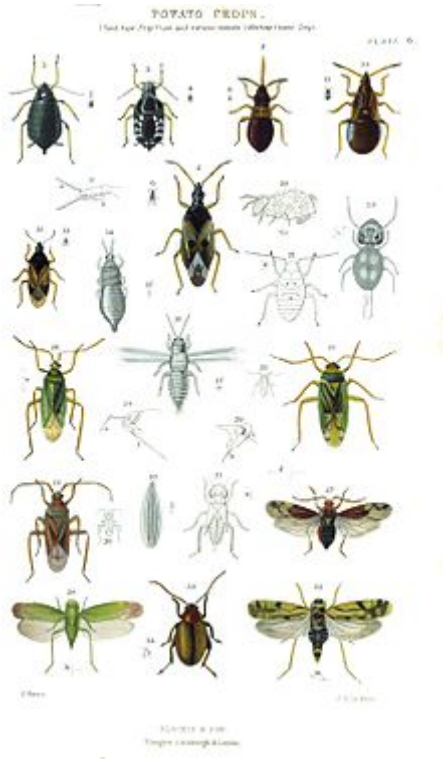
In the 18th century many works were published on agriculture. Many contained accounts of pest insects. In France Claude Sionnest (1749–1820) was a notable figure.

19th century

In Britain, John Curtis wrote the influential 1860 treatise *Farm Insects*, dealing with the insect pests of corn, roots, grass and stored grain. Fruit and pests were described by authors such as Saunders, Joseph Albert Lintner, Eleanor Anne Ormerod, Charles Valentine Riley, Mark Vernon Slingerland in America and Canada. The pioneers in Europe were Ernst Ludwig Taschenberg, Sven Lampa (1839–1914), Enzio Reuter (1867–1951) and Vincenze Kollar. Charles French (1842–1933), Walter Wilson Froggatt (1858–1937) and Henry Tryon (1856–1943) pioneered in Australia. [2]

It was not until the last quarter of the 19th century that any real advance was made in the study of economic entomology. Among the early writings, besides the book of Curtis, there was a publication by Pohl and Kollar, entitled *Insects Injurious to Gardeners, Foresters and Farmers*, published in 1837, and Taschenberg's *Praktische Insecktenkunde*.[2] During the 19th century Italian entomologists made significant progress in controlling diseases of the silkworm moth, in the control of agricultural pests and in stored product entomology. Significant figures were: Agostino Bassi (1773–1856), Camillo Róndani (1808–1879), Adolfo Targioni Tozzetti (1823–1902), Pietro Stefanelli (1835, 1919), Camillo Acqua (1863–1936) Antonio Berlese (1863–1927), Gustavo Leonardi(1869–1918) and Enrico Verson (1845–1927). In France Etienne Laurent Joseph Hippolyte Boyer de Fonscolombe, Charles Jean-Baptiste Amyot, Émile Blanchard, Valéry Mayet and Claude Charles Goureau were early workers, as was Jean Victoire Audouin, the author of *Histoire des insectes nuisibles à la vigne et particulièrement de la Pyrale*, Philippe Alexandre Jules Künckel d'Herculais, Joseph Jean Baptiste Géhin and Jean-Étienne Girard. American literature began as far back as 1788, when a report on the Hessian fly was issued by Sir Joseph Banks; in 1817 Thomas Say began his writings; while in 1856

Asa Fitch started his report on *Noxious Insects of New York*.[2] Also in America, Matthew Cooke wrote *Treatise on the Insects Injurious to Fruit and Fruit Trees of the State of California, and Remedies Recommended for Their Extermination*, published in 1881.[3] The Englishman Frederick Vincent Theobald wrote A textbook of agricultural zoology in 1890. It became a standard text worldwide. Notable foresters were Herman von Nördlinger (1818–1897) and Julius Theodor Christian Ratzeburg (1801–1871).



"Insects infesting potato crops": a plate from John Curtis's *Farm Insects*, 1860

20th century

Among the most important reports early in the 20th century were those of Charles Valentine Riley, published by the U.S. Department of Agriculture, extending from 1878 to his death, in which is embodied an enormous amount of valuable material. At his death the work fell to Professor Leland Ossian Howard, in the form of *Bulletin of the U.S. Department of Agriculture*. The chief writings of J. A. Lintner extend from 1882 to 1898, in yearly parts, under the title of *Reports on the Injurious Insects of the State of New York*.[2] Another significant contributor to the entomological literature of the United States was Charles W. Woodworth. The Florida entomologist Wilmon Newell was a pioneer of pest control as was Clarence Preston Gillette. In India Thomas Bainbrigge Fletcher, who succeeded Harold Maxwell-Lefroy and Lionel de Nicéville as Imperial Entomologist, wrote *Some South Indian insects and other animals of importance considered especially from an economic point of view*, an influential work in the subcontinent. In France Alfred Balachowsky was a key figure. In the last quarter of the 20th century new techniques were pioneered and new theories developed, for instance Integrated Pest Management by Ray F. Smith.

Harmful insects

Insects considered *pests* of some sort occur among all major living orders with the exception of Ephemeroptera (mayflies), Odonata, Plecoptera (stoneflies), Embioptera (webspinners), Trichoptera (caddisflies), Neuroptera (in the broad sense), and Mecoptera (also, the tiny groups Zoraptera, Grylloblattodea, and Mantophasmatodea). Conversely, of course, essentially all insect orders primarily have members which are beneficial, in some respects, with the exception of Phthiraptera (lice), Siphonaptera (fleas), and Strepsiptera, the three orders whose members are exclusively parasitic.


The phylloxera, a true gourmet, finds out the best vineyards and attaches itself to the best wines
Cartoon from Punch, 6 September 1890

Insects are considered pests for a variety of reasons, including direct damage by feeding on crop plants in the field or by infesting stored products, indirect damage by spreading viral diseases of crop plants (especially by sucking insects such as leafhoppers), spreading disease among humans and livestock, and annoyance to humans. Examples of insects regarded as pests include the phylloxera, migratory locusts, the Colorado potato beetle, the boll weevil, Japanese beetle, aphids, mosquitoes, cockroaches, the Western corn rootworm, and some fly species.

In the past entomologists working on pest insects attempted to eradicate species. This rarely worked except in islands or controlled environments and raised ethical issues. Over time the language changed to terms like *control* and *management*. The indiscriminate use of toxic and persistent chemicals and the resurgence of pests in the history of cotton growing in the US has been particularly well studied.

Beneficial insects

Honey is perhaps the most economically valuable product from insects. Beekeeping is a commercial enterprise in most parts of the world and many forest tribes have been dependent on honey as a major source of nutrition. Honeybees can also act as pollinators of crop species. Many predators and parasitoid insects are encouraged and augmented in modern agriculture.

Silk is extracted from both reared caterpillars as well as from the wild (producing wild silk). Sericulture deals with the techniques for efficient silkworm rearing and silk production. Although new fabric materials have substituted silk in many applications, it continues to be the material of choice for surgical sutures.

Lac was once extracted from scale insects but is now replaced by synthetic substitutes. The dye extracted from cochineal insects was similarly replaced by technological advances.

The idea of insects as human food, entomophagy, widely practised in traditional societies, has been proposed as a solution to meet the growing demand for food, but has not gained widespread acceptance in the West.



Boll Weevil Monument, erected by the citizens of Enterprise, Alabama to honour the pest that ended their dependence on cotton, a poverty crop

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Storage pest

A **storage pest** is an insect or other animal that damages or destroys stored food or other stored valuable organic matter.[1] Insects are a large proportion of storage pests with each type of crop having specific insects that gravitate towards them such as the genus *Tribolium* that consists of insects such as *Tribolium castaneum* (red flour beetle) or *Tribolium confusum* (confused flour beetle) which damage flour crops primarily.[2][3]

Contents

Insects
- Types of Insect Pests
 - Primary Pests
 - Lesser grain borer (*Rhyzopertha dominica*)
 - Rice weevil (*Sitophilus oryzae*)
 - Secondary Pests
 - Rust-red flour beetle (*Tribolium castaneum*)
 - Warehouse moth (*Ephestia spp*)

References

Insects

Many insects act as storage pests in crops including grain crops, and destroy approximately 25-33% of crops worldwide, each year.[3] Crops can be completely destroyed or even partially damaged affecting the quality of the crop and the ability to germinate new ones, by decreasing the protein content and removing the seeds from the grains.

Types of Insect Pests

There are two types of grain insect pests, primary and secondary pests.



Lesser grain borer (*Rhyzopertha dominica*).

Primary Pests

Primary grain pests attack the whole grain. The eggs are laid outside the grain, before the larvae mature inside the grain and then chew their way out. Some of these pets include the Lesser grain borer, Granary weevil and Rice weevil.[3]

Lesser grain borer (*Rhyzopertha dominica*)

The lesser grain borer has a dark coloured cylindrical structure with the head concealed.[4] When lesser grain borer eggs are laid, they are laid outside the grain, however mature inside the shell of the seed which can take up to 6 weeks if the temperature is cooler, with the adult borers not living for longer than two months. This species is known to damage stored wheat, corn and cereal crops with the seeds become hollowed out husks. Products with small infestations should be discarded however the grains can be treated with smaller amounts of spray. However, large infestations require more control, including complete fumigation.

Rice weevil (*Sitophilus oryzae*)

The adult rice weevil has an orange-black exoskeleton and lays up to 450 eggs in pores of the damaged grains with each hatched egg further damaging the grain from the inside. Similarly to the lesser grain borer, maturation also happens inside the grain with the matured adult rice weevil eating through the husk of the grain to get out. The life cycle is similar to that of the lesser grain borer in summer months (approximately one month) and adult weevils live up to 8 months after the experience their life cycle.[3]



Rice weevil (*Sitophilus oryzae*).

Secondary Pests

Secondary grain insects feed on broken grain and any powder products left as a result of the broken grain. These pests include the genus *Tribolium*, beetle species and moth species.

Rust-red flour beetle (*Tribolium castaneum*)

The Rust-red flour beetle is a red-brown beetle with an exoskeleton that darkens in colour as the beetle increases in age, with the maximum adult age being a year. Unlike primary pests, Rust-red flour beetles can produce up to 1000 eggs and lay them inside the damaged grain with parts of the larvae able to use the damaged grains and cereal as their food source.[3]



Rust-red flour beetle (*Tribolium castaneum*).

Warehouse moth (*Ephestia spp*)

The Warehouse moth is a grey moth that remains on the surface of the grain with the female moth laying up to 200 eggs, however their life span is only 2 weeks long with a 4 week life cycle. Similarly to other secondary pests, the Warehouse moth eggs use the surface of the grain, although when the larvae hatch they leave a stream of silk that encapsulates the surface of the grain which can then be used as a cocoon for mature larvae.[3]



Warehouse moth (*Ephestia spp*).

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List of pest-repelling plants

This **list of pest-repelling plants** includes plants utilised for their ability to repel insects, nematodes, and other pests. They have been used in companion planting as pest control in agricultural and garden situations, and in households.

Certain plants have shown effectiveness as topical repellents for haematophagous insects, such as the use of lemon eucalyptus in PMD, but incomplete research and misunderstood applications can produce variable results.[1]

The essential oils of many plants are also well known for their pest-repellent properties. Oils from the families Lamiaceae (mints), Poaceae (true grasses), and Pinaceae (pines) are common haematophagous insect repellents worldwide.[1]

Plants that can be planted or used fresh to repel pests include:

Plant	Pests
artemisias	repels insects,[2] including ants, cabbage looper, cabbage maggot, carrot fly, codling moth, flea beetles, whiteflies, the Cabbage White, and the Small White, as well as mice[3]
basil	repels flies, including mosquitoes[2][4] the carrot fly, asparagus beetles and whiteflies[3]
borage	*repels tomato hornworm and cabbage worms*[2]
castor bean	repels moles[3]
catnip	repels ants, flea beetles, aphids, the Japanese beetle, squash bugs, weevils,[2] the Colorado potato beetle, the cabbage looper,[3] and cockroaches.[4] May attract cats.
chamomile	repels flying insects[4]
chives	repels carrot fly, Japanese beetle,[2] and aphids[3]
chrysanthemums	repel roaches, ants, the Japanese beetle, ticks, silverfish, lice, fleas, bedbugs, and root-knot nematodes[2]
citronella grass	repels insects, may deter cats[5]
~~citrosa~~	proven not to repel mosquitoes[6]
clovers	repel aphids and wireworms[3]
common lantana	repels mosquitoes[1]
coriander	repels aphids, Colorado potato beetle, and spider mites[3]
cosmos	repel the corn earworm
crown imperial	repel rabbits, mice, moles, voles and ground squirrels[7]
dahlias	repel nematodes[2]
dill	repels aphids, squash bugs, spider mites,[2] the cabbage looper, and the Small White[3]
eucalyptus	repels aphids, the cabbage looper, and the Colorado potato beetle[3]
fennel	repels aphids, slugs, and snails[3]
fever tea	repels mosquitoes[1]
four o'clocks	attract and poison the Japanese beetle[2]
French marigold	repels whiteflies, kills nematodes[2]
garlic	repels root maggots,[2] cabbage looper, Mexican bean beetle, and peach tree borer.
geraniums	repel leafhoppers, the corn earworm, and the Small White[3]
hyssop	repels the cabbage looper and the Small White[3]
larkspurs	repel aphids[3]
lavender	repels moths, scorpions, water scorpions, fleas, and flies, including mosquitoes[4]
leek	repels carrot fly[3]
lemongrass	repels mosquitoes[8]
lemon balm	repels mosquitoes[4]
lemon thyme	repels mosquitoes[4]
lettuce	repels carrot fly[3]
lime basil	repels mosquitoes[1]

Mexican marigold	repels insects and rabbits[2]
myrrh	repels insects[5]
narcissus	repel moles[3]
nasturtiums	repel squash bugs,[2] aphids (though there is conflicting information with some sources stating it attracts aphids),[9] many beetles, and the cabbage looper[3]
onion	repels rabbits, the cabbage looper, and the Small White[3]
oregano	repellent to many pests[3]
parsley	repels asparagus beetles[3]
peppermint	repels aphids, cabbage looper, flea beetles, squash bugs, whiteflies, and the Small White[3]
petunias	repel aphids, tomato hornworm, asparagus beetles, leafhoppers,[2] and squash bugs[3]
pitcher plants	traps and ingests insects
radish	repels cabbage maggot and cucumber beetles[3]
rosemary	repels cabbage looper, carrot fly, cockroaches and mosquitoes[10], slugs, snails, as well as the Mexican bean beetle[3]
rue	repels cucumber and flea beetles
Sarracenia pitcher plants	are especially proficient at trapping yellowjacket wasps
spearmint	repels fleas, moths, ants, beetles, rodents,[4] aphids, squash bugs, and the cabbage looper[3]
spiny amaranth	repels cutworms
stone root	repels mosquitoes[5]
summer savory	repels bean beetles[3]
tansy	repels ants, many beetles and flies, squash bugs, cutworms, Small White, and Cabbage White[3]
thyme	repels cabbage looper, cabbage maggot, corn earworm, whiteflies, tomato hornworm, and Small White
tobacco	repels carrot fly, flea beetles and worms.[3]
tomato	repels asparagus beetles[3]
venus flytrap	ingests insects[4]

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Integrated pest management

Integrated pest management (IPM), also known as **integrated pest control (IPC)** is a broad-based approach that integrates practices for economic control of pests. IPM aims to suppress pest populations below the economic injury level (EIL). The UN's Food and Agriculture Organization defines IPM as "the careful consideration of all available pest control techniques and subsequent integration of appropriate measures that discourage the development of pest populations and keep pesticides and other interventions to levels that are economically justified and reduce or minimize risks to human health and the environment. IPM emphasizes the growth of a healthy crop with the least possible disruption to agro-ecosystems and encourages natural pest control mechanisms."[1] Entomologists and ecologists have urged the adoption of IPM pest control since the 1970s.[2] IPM allows for safer pest control.



An IPM boll weevil trap in a cotton field (Manning, South Carolina).

The introduction and spread of invasive species can also be managed with IPM by reducing risks while maximizing benefits and reducing costs.[3][4][5]

Contents

History
Applications
Principles
Process
Southeast Asia
See also
References
Further reading
External links

History

Shortly after World War II, when synthetic insecticides became widely available, entomologists in California developed the concept of "supervised insect control".[6] Around the same time, entomologists in the US Cotton Belt were advocating a similar approach. Under this scheme, insect control was "supervised" by qualified entomologists and insecticide applications were based on conclusions reached from periodic monitoring of pest and natural-enemy populations. This was viewed as an alternative to calendar-based programs. Supervised control was based on knowledge of the ecology and analysis of projected trends in pest and natural-enemy populations.

Supervised control formed much of the conceptual basis for the "integrated control" that University of California entomologists articulated in the 1950s. Integrated control sought to identify the best mix of chemical and biological controls for a given insect pest. Chemical insecticides were to be used in the manner least disruptive to biological control. The term "integrated" was thus

synonymous with "compatible." Chemical controls were to be applied only after regular monitoring indicated that a pest population had reached a level (the economic threshold) that required treatment to prevent the population from reaching a level (the economic injury level) at which economic losses would exceed the cost of the control measures.

IPM extended the concept of integrated control to all classes of pests and was expanded to include all tactics. Controls such as pesticides were to be applied as in integrated control, but these now had to be compatible with tactics for all classes of pests. Other tactics, such as host-plant resistance and cultural manipulations, became part of the IPM framework. IPM combined entomologists, plant pathologists, nematologists and weed scientists.

In the United States, IPM was formulated into national policy in February 1972 when President Richard Nixon directed federal agencies to take steps to advance the application of IPM in all relevant sectors. In 1979, President Jimmy Carter established an interagency IPM Coordinating Committee to ensure development and implementation of IPM practices.[7]

Perry Adkisson and Ray F. Smith received the 1997 World Food Prize for encouraging the use of IPM.[8]

Applications

IPM is used in agriculture, horticulture, forestry, human habitations, preventive conservation and general pest control, including structural pest management, turf pest management and ornamental pest management.

Principles

An American IPM system is designed around six basic components:[9]

- **Acceptable pest levels**—The emphasis is on *control*, not *eradication*. IPM holds that wiping out an entire pest population is often impossible, and the attempt can be expensive and unsafe. IPM programmes first work to establish acceptable pest levels, called action thresholds, and apply controls if those thresholds are crossed. These thresholds are pest and site specific, meaning that it may be acceptable at one site to have a weed such as white clover, but not at another site. Allowing a pest population to survive at a reasonable threshold reduces selection pressure. This lowers the rate at which a pest develops resistance to a control, because if almost all pests are killed then those that have resistance will provide the genetic basis of the future population. Retaining a significant number of unresistant specimens dilutes the prevalence of any resistant genes that appear. Similarly, the repeated use of a single class of controls will create pest populations that are more resistant to that class, whereas alternating among classes helps prevent this.
- **Preventive cultural practices**—Selecting varieties best for local growing conditions and maintaining healthy crops is the first line of defense. Plant quarantine and 'cultural techniques' such as crop sanitation are next, e.g., removal of diseased plants, and cleaning pruning shears to prevent spread of infections. Beneficial fungi and bacteria are added to the potting media of horticultural crops vulnerable to root diseases, greatly reducing the need for fungicides.
- **Monitoring**—Regular observation is critically important. Observation is broken into inspection and identification.[10] Visual inspection, insect and spore traps, and other methods are used to monitor pest levels. Record-keeping is essential, as is a thorough knowledge of target pest behavior and reproductive cycles. Since insects are cold-blooded, their physical development is dependent on area temperatures. Many insects have had their development cycles modeled in terms of degree-days. The degree days of an environment determines the optimal time for a specific insect outbreak. Plant pathogens follow similar patterns of response to weather and season.
- **Mechanical controls**—Should a pest reach an unacceptable level, mechanical methods are the first options. They include simple hand-picking, barriers, traps, vacuuming and tillage to disrupt breeding.
- **Biological controls**—Natural biological processes and materials can provide control, with acceptable environmental impact, and often at lower cost. The main approach is to promote beneficial insects that eat or parasitize target pests. Biological insecticides, derived from naturally occurring microorganisms (*e.g.*—*Bt*, entomopathogenic fungi and entomopathogenic nematodes), also fall in this category. Further 'biology-based' or 'ecological' techniques are under evaluation.
- **Responsible use**—Synthetic pesticides are used as required and often only at specific times in a pest's life cycle. Many newer pesticides are derived from plants or naturally occurring substances (*e.g.*—nicotine, pyrethrum and insect juvenile hormone analogues), but the toxophore or active component may be altered to provide increased biological activity or stability. Applications of pesticides must reach their intended targets.

> Matching the application technique to the crop, the pest, and the pesticide is critical. The use of low-volume spray equipment reduces overall pesticide use and labor cost.

An IPM regime can be simple or sophisticated. Historically, the main focus of IPM programmes was on agricultural insect pests.[11] Although originally developed for agricultural pest management, IPM programmes are now developed to encompass diseases, weeds and other pests that interfere with management objectives for sites such as residential and commercial structures, lawn and turf areas, and home and community gardens.

Process

IPM is the selection and use of pest control actions that will ensure favourable economic condition, ecological and social consequences[12] and is applicable to most agricultural, public health and amenity pest management situations. The IPM process starts with monitoring, which includes inspection and identification, followed by the establishment of economic injury levels. The economic injury levels set the economic threshold level. That is the point when pest damage (and the benefits of treating the pest) exceed the cost of treatment.[13] This can also be an action threshold level for determining an unacceptable level that is not tied to economic injury. Action thresholds are more common in structural pest management and economic injury levels in classic agricultural pest management. An example of an action threshold is one fly in a hospital operating room is not acceptable, but one fly in a pet kennel would be acceptable. Once a threshold has been crossed by the pest population action steps need to be taken to reduce and control the pest. Integrated pest management employs a variety of actions including cultural controls such as physical barriers, biological controls such as adding and conserving natural predators and enemies of the pest, and finally chemical controls or pesticides. Reliance on knowledge, experience, observation and integration of multiple techniques makes IPM appropriate for organic farming (excluding synthetic pesticides). These may or may not include materials listed on the Organic Materials Review Institute (OMRI)[14] Although the pesticides and particularly insecticides used in organic farming and organic gardening are generally safer than synthetic pesticides, they are not always more safe or environmentally friendly than synthetic pesticides and can cause harm.[15] For conventional farms IPM can reduce human and environmental exposure to hazardous chemicals, and potentially lower overall costs.

Risk assessment usually includes four issues: 1) characterization of biological control agents, 2) health risks, 3) environmental risks and 4) efficacy.[16]

Mistaken identification of a pest may result in ineffective actions. E.g., plant damage due to over-watering could be mistaken for fungal infection, since many fungal and viral infections arise under moist conditions.

Monitoring begins immediately, before the pest's activity becomes significant. Monitoring of agricultural pests includes tracking soil/planting media fertility and water quality. Overall plant health and resistance to pests is greatly influenced by pH, alkalinity, of dissolved mineral and oxygen reduction potential. Many diseases are waterborne, spread directly by irrigation water and indirectly by splashing.

Once the pest is known, knowledge of its lifecycle provides the optimal intervention points.[17] For example, weeds reproducing from last year's seed can be prevented with mulches and pre-emergent herbicide.

Pest-tolerant crops such as soybeans may not warrant interventions unless the pests are numerous or rapidly increasing. Intervention is warranted if the expected cost of damage by the pest is more than the cost of control. Health hazards may require intervention that is not warranted by economic considerations.

Specific sites may also have varying requirements. E.g., white clover may be acceptable on the sides of a tee box on a golf course, but unacceptable in the fairway where it could confuse the field of play.[18]

Possible interventions include mechanical/physical, cultural, biological and chemical. Mechanical/physical controls include picking pests off plants, or using netting or other material to exclude pests such as birds from grapes or rodents from structures. Cultural controls include keeping an area free of conducive conditions by removing waste or diseased plants, flooding, sanding,

and the use of disease-resistant crop varieties.[12] Biological controls are numerous. They include: conservation of natural predators or augmentation of natural predators, sterile insect technique (SIT).[19]

Augmentation, inoculative release and inundative release are different methods of biological control that affect the target pest in different ways. Augmentative control includes the periodic introduction of predators.[20][21][22][23][24] With inundative release, predators are collected, mass-reared and periodically released in large numbers into the pest area.[25][26][27] This is used for an immediate reduction in host populations, generally for annual crops, but is not suitable for long run use.[28] With inoculative release a limited number of beneficial organisms are introduced at the start of the growing season. This strategy offers long term control as the organism's progeny affect pest populations throughout the season and is common in orchards.[28][29] With seasonal inoculative release the beneficials are collected, mass-reared and released seasonally to maintain the beneficial population. This is commonly used in greenhouses.[29] In America and other western countries, inundative releases are predominant, while Asia and the eastern Europe more commonly use inoculation and occasional introductions.[28]

The sterile insect technique (SIT) is an area-wide IPM program that introduces sterile male pests into the pest population to trick females into (unsuccessful) breeding encounters, providing a form of birth control and reducing reproduction rates.[19] The biological controls mentioned above only appropriate in extreme cases, because in the introduction of new species, or supplementation of naturally occurring species can have detrimental ecosystem effects. Biological controls can be used to stop invasive species or pests, but they can become an introduction path for new pests.[30]

Chemical controls include horticultural oils or the application of insecticides and herbicides. A green pest management IPM program uses pesticides derived from plants, such as botanicals, or other naturally occurring materials.

Pesticides can be classified by their modes of action. Rotating among materials with different modes of action minimizes pest resistance.[12]

Evaluation is the process of assessing whether the intervention was effective, whether it produced unacceptable side effects, whether to continue, revise or abandon the program.[31]

Southeast Asia

The Green Revolution of the 1960s and '70s introduced sturdier plants that could support the heavier grain loads resulting from intensive fertilizer use. Pesticide imports by 11 Southeast Asian countries grew nearly sevenfold in value between 1990 and 2010, according to FAO statistics, with disastrous results. Rice farmers become accustomed to spraying soon after planting, triggered by signs of the leaf folder moth, which appears early in the growing season. It causes only superficial damage and doesn't reduce yields. In 1986, Indonesia banned 57 pesticides and completely stopped subsidizing their use. Progress was reversed in the 2000s, when growing production capacity, particularly in China, reduced prices. Rice production in Asia more than doubled. But it left farmers believing more is better—whether it's seed, fertilizer, or pesticides.[32]

The brown planthopper, *Nilaparvata lugens*, the farmers' main target, has become increasingly resistant. Since 2008, outbreaks have devastated rice harvests throughout Asia, but not in the Mekong Delta. Reduced spraying allowed natural predators to neutralize planthoppers in Vietnam. In 2010 and 2011, massive planthopper outbreaks hit 400,000 hectares of Thai rice fields, causing losses of about $64 million. The Thai government is now pushing the "no spray in the first 40 days" approach.[32]

By contrast early spraying kills frogs, spiders, wasps and dragonflies that prey on the later-arriving and dangerous planthopper and produced resistant strains. Planthoppers now require pesticide doses 500 times greater than originally. Overuse indiscriminately kills beneficial insects and decimates bird and amphibian populations. Pesticides are suspected of harming human health and became a common means for rural Asians to commit suicide.[32]

In 2001, scientists challenged 950 Vietnamese farmers to try IPM. In one plot, each farmer grew rice using their usual amounts of seed and fertilizer, applying pesticide as they chose. In a nearby plot, less seed and fertilizer were used and no pesticides were applied for 40 days after planting. Yields from the experimental plots was as good or better and costs were lower, generating 8% to 10% more net income. The experiment led to the "three reductions, three gains" campaign, claiming that cutting the use of seed, fertilizer and pesticide would boost yield, quality and income. Posters, leaflets, TV commercials and a 2004 radio soap opera that featured a rice farmer who gradually accepted the changes. It didn't hurt that a 2006 planthopper outbreak hit farmers using insecticides harder than those who didn't. Mekong Delta farmers cut insecticide spraying from five times per crop cycle to zero to one.

The Plant Protection Center and the International Rice Research Institute (IRRI) have been encouraging farmers to grow flowers, okra and beans on rice paddy banks, instead of stripping vegetation, as was typical. The plants attract bees and a tiny wasp that eats planthopper eggs, while the vegetables diversify farm incomes.[32]

Agriculture companies offer bundles of pesticides with seeds and fertilizer, with incentives for volume purchases. A proposed law in Vietnam requires licensing pesticide dealers and government approval of advertisements to prevent exaggerated claims. Insecticides that target other pests, such as *Scirpophaga incertulas* (stem borer), the larvae of moth species that feed on rice plants allegedly yield gains of 21% with proper use.[32]

See also

- Agroecology
- Agronomy
- Biodynamic agriculture
- Endangered arthropod
- Forest integrated pest management
- International Organization for Biological Control
- Pesticide application
- Professional Landcare Network (PLANET)
- Push-pull technology
- Soil contamination
- Sustainable agriculture

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External links

- Introducing to Integrated Pest Management (https://www.epa.gov/managing-pests-schools/introduction-integrated-pest-management) via EPA

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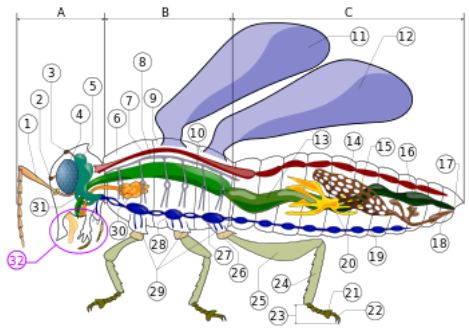
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Insect morphology

Insect morphology is the study and description of the physical form of insects. The terminology used to describe insects is similar to that used for other arthropods due to their shared evolutionary history. Three physical features separate insects from other arthropods: they have a body divided into three regions (head, thorax, and abdomen), have three pairs of legs, and mouthparts located *outside* of the head capsule. It is this position of the mouthparts which divides them from their closest relatives, the non-insect hexapods, which includes Protura, Diplura, and Collembola.

There is enormous variation in body structure amongst insect species. Individuals can range from 0.3 mm (fairyflies) to 30 cm across (great owlet moth);[1]:7 have no eyes or many; well-developed wings or none; and legs modified for running, jumping, swimming, or even digging. These modifications allow insects to occupy almost every ecological niche on the planet, except the deep ocean and the Antarctic. This article describes the basic insect body and some of the major variations of the different body parts; in the process it defines many of the technical terms used to describe insect bodies.



Insect morphology

Legend of body parts

Tagmata: A - Head, B - Thorax, C - Abdomen.

1. antenna
2. ocelli (lower)
3. ocelli (upper)
4. compound eye
5. brain (cerebral ganglia)
6. prothorax
7. dorsal blood vessel
8. tracheal tubes (trunk with spiracle)
9. mesothorax
10. metathorax
11. forewing
12. hindwing
13. mid-gut (stomach)
14. dorsal tube (heart)
15. ovary
16. hind-gut (intestine, rectum & anus)
17. anus
18. oviduct
19. nerve cord (abdominal ganglia)
20. Malpighian tubes
21. tarsal pads
22. claws
23. tarsus
24. tibia
25. femur
26. trochanter
27. fore-gut (crop, gizzard)
28. thoracic ganglion
29. coxa
30. salivary gland
31. subesophageal ganglion
32. mouthparts

Contents

Anatomy summary

External
- Exoskeleton
- Head
 - Compound eyes and ocelli
 - Antennae
 - Mouthparts
 - Mandibulate
 - Piercing-sucking
 - Siphoning
 - Sponging
- Thorax
 - Prothorax
 - Pterothorax
 - Wings
 - Internal
 - Veins
 - Fields
 - Joints
 - Coupling, folding, and other features
 - Legs
- Abdomen
 - External genitalia

Internal
- Nervous system
- Digestive system
 - Foregut
 - Midgut
 - Hindgut
- Respiratory systems
- Circulatory system
- Endocrine system
- Reproductive system
 - Female
 - Male

Internal morphology of different taxa
- Blattodea
- Coleoptera
- Dermaptera
- Diptera
- Lepidoptera

See also

References

Anatomy summary

Insects, like all arthropods, have no interior skeleton; instead, they have an exoskeleton, a hard outer layer made mostly of chitin which protects and supports the body. The insect body is divided into three parts: the head, thorax, and abdomen.[2] The head is specialized for sensory input and food intake; the thorax, which is the anchor point for the legs and wings (if present), is specialized for locomotion; and the abdomen for digestion, respiration, excretion, and reproduction.[1]:22–48 Although the general function of the three body regions is the same across all insect species, there are major differences in basic structure, with wings, legs, antennae, and mouthparts being highly variable from group to group.[3]

External

Exoskeleton

The insect outer skeleton, the cuticle, is made up of two layers; the epicuticle, which is a thin, waxy, water-resistant outer layer and contains no chitin, and the layer under it called the procuticle. This is chitinous and much thicker than the epicuticle and has two layers, the outer is the exocuticle while the inner is the endocuticle. The tough and flexible endocuticle is built from numerous layers of fibrous chitin and proteins, criss-crossing each other in a sandwich pattern, while the exocuticle is rigid and sclerotized.[1]:22–24 The exocuticle is greatly reduced in many soft-bodied insects, especially the larval stages (e.g., caterpillars). Chemically, chitin is a long-chain polymer of a N-acetylglucosamine, a derivative of glucose. In its unmodified form, chitin is translucent, pliable, resilient and quite tough. In arthropods, however, it is often modified, becoming embedded in a hardened proteinaceous matrix, which forms much of the exoskeleton. In its pure form, it is leathery, but when encrusted in calcium carbonate, it becomes much harder.[4] The difference between the unmodified and modified forms can be seen by comparing the body wall of a caterpillar (unmodified) to a beetle (modified).

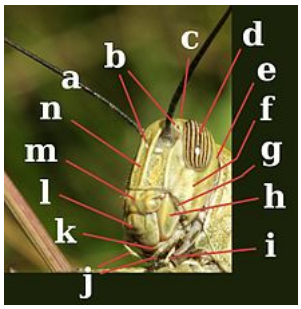
From the embryonic stages itself, a layer of columnar or cuboidal epithelial cells gives rise to the external cuticle and an internal basement membrane. The majority of insect material is held in the endocuticle. The cuticle provides muscular support and acts as a protective shield as the insect develops. However, since it cannot grow, the external sclerotised part of the cuticle is periodically shed in a process called "moulting". As the time for moulting approaches, most of the exocuticle material is reabsorbed. In moulting, first the old cuticle separates from the epidermis (apolysis). Enzymatic moulting fluid is released between the old cuticle and epidermis, which separates the exocuticle by digesting the endocuticle and sequestering its material for the new cuticle. When the new cuticle has formed sufficiently, the epicuticle and reduced exocuticle are shed in ecdysis.[5]:16–20

The four principal regions of an insect body segment are: tergum or dorsal, sternum or ventral and the two pleura or laterals. Hardened plates in the exoskeleton are called sclerites, which are subdivisions of the major regions - tergites, sternites and pleurites, for the respective regions tergum, sternum, and pleuron.[6]

Head

The head in most insects is enclosed in a hard, heavily sclerotized, exoskeletal **head capsule'**. The main exception is in those species whose larvae are not fully sclerotised, mainly some holometabola; but even most unsclerotised or weakly sclerotised larvae tend to have well sclerotised head capsules, for example the larvae of Coleoptera and Hymenoptera. The larvae of Cyclorrhapha however, tend to have hardly any head capsule at all.

The head capsule bears most of the main sensory organs, including the antennae, ocelli, and the compound eyes. It also bears the mouthparts. In the adult insect the head capsule is apparently unsegmented, though embryological studies show it to consist of six segments that bear the paired head appendages, including the mouthparts, each pair on a specific segment.[7] Each such pair occupies one segment, though not all segments in modern insects bear any visible appendages.



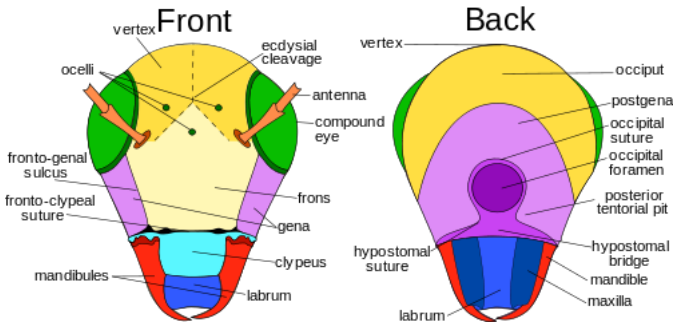
Head of Orthoptera, Acrididae. **a**:antenna; **b**:ocelli; **c**:vertex; **d**:compound eye; **e**:occiput; **f**:gena; **g**:pleurostoma; **h**:mandible; **i**:labial palp; **j**:maxillary palps; **k**:maxilla; **l**:labrum; **m**:clypeus; **n**:frons

Of all the insect orders, Orthoptera most conveniently display the greatest variety of features found in the heads of insects, including the sutures and sclerites.[6] Here, the vertex, or the apex (dorsal region), is situated between the compound eyes for insects with hypognathous and opisthognathous heads. In prognathous insects, the vertex is not found between the compound eyes, but rather, where the ocelli are normally found. This is because the primary axis of the head is rotated 90° to become parallel to the primary axis of the body. In some species, this region is modified and assumes a different name.[8]:13

The ecdysial suture is made of the coronal, frontal, and epicranial sutures plus the ecdysial and cleavage lines, which vary among different species of insects. The ecdysial suture is longitudinally placed on the vertex and separates the epicranial halves of the head to the left and right sides. Depending on the insect, the suture may come in different shapes: like either a Y, U, or V. Those diverging lines that make up the ecdysial suture are called the frontal or **frontogenal** sutures. Not all species of insects have frontal sutures, but in those that do, the sutures split open during ecdysis, which helps provide an opening for the new instar to emerge from the integument.


Larva of beetle, family Cerambycidae, showing sclerotised epicranium; rest of body hardly sclerotised

The frons is that part of the head capsule that lies ventrad or anteriad of the vertex. The frons varies in size relative to the insect, and in many species the definition of its borders is arbitrary, even in some insect taxa that have well-defined head capsules. In most species, though, the frons is bordered at its anterior by the frontoclypeal or epistomal sulcus above the clypeus. Laterally it is limited by the fronto-genal sulcus, if present, and the boundary with the vertex, by the ecdysial cleavage line, if it is visible. If there is a median ocellus, it generally is on the frons, though in some insects such as many Hymenoptera, all three ocelli appear on the vertex. A more formal definition is that it is the sclerite from which the pharyngeal dilator muscles arise, but in many contexts that too, is not helpful.[7] In the anatomy of some taxa, such as many Cicadomorpha, the front of the head is fairly clearly distinguished and tends to be broad and sub-vertical; that median area commonly is taken to be the frons.[9]



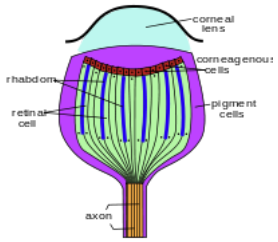

Larva of Syrphid fly, member of Cyclorrhapha, without epicranium, almost without sclerotisation apart from its jaws.

The clypeus is a sclerite between the face and labrum, which is dorsally separated from the frons by the frontoclypeal suture in primitive insects. The clypeogenal suture laterally demarcates the clypeus, with the clypeus ventrally separated from the labrum by the clypeolabral suture. The clypeus differs in shape and size, such as species of Lepidoptera with a large clypeus with elongated mouthparts. The cheek or gena forms the sclerotized area on each side of the head below the compound eyes extending to the gular suture. Like many of the other parts making up the insect's head, the gena varies among species, with its boundaries difficult to establish. For example, in dragonflies and damselflies, it is between the compound eyes, clypeus, and mouthparts. The postgena is the area immediately posteriad, or posterior or lower on the gena of pterygote insects, and forms the lateral and ventral parts of the occipital arch. The occipital arch is a narrow band forming the posterior edge of the head capsule arching dorsally over the foramen. The subgenal area is usually narrow, located above the mouthparts; this area also includes the hypostoma and pleurostoma.[8]:13–14 The vertex extends anteriorly above the bases of the antennae as a prominent, pointed, concave rostrum. The posterior wall of the head capsule is penetrated by a large aperture, the foramen. Through it pass the organ systems, such as nerve cord, esophagus, salivary ducts, and musculature, connecting the head with the thorax.[10]

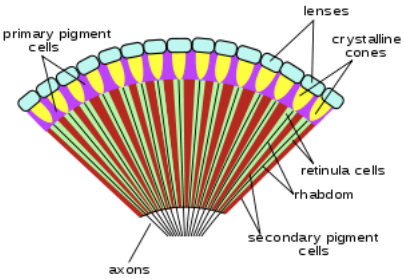
On the posterior aspect of the head are the occiput, postgena, occipital foramen, posterior tentorial pit, gula, postgenal bridge, hypostomal suture and bridge, and the mandibles, labium, and maxilla. The occipital suture is well founded in species of Orthoptera, but not so much in other orders. Where found, the occipital suture is the arched, horseshoe-shaped groove on the back of the head, ending at the posterior of each mandible. The postoccipital suture is a landmark on the posterior surface of the head, and is typically near the occipital foremen. In pterygotes, the postocciput forms the extreme posterior, often U-shaped, which forms the rim of the head extending to the postoccipital suture. In pterygotes, such as those of Orthoptera, the occipital foramen and the mouth are not separated. The three types of occipital closures, or points under the occipital foramen that separate the two lower halves of the postgena, are: the hypostomal bridge, the postgenal bridge, and the gula. The hypostomal bridge is usually found in insects with hypognathous orientation. The postgenal bridge is found in the adults of species of higher Diptera and aculeate Hymenoptera, while the gula is found on some Coleoptera, Neuroptera, and Isoptera, which typically display prognathous-oriented mouthparts.[8]:15

Compound eyes and ocelli

Most insects have one pair of large, prominent compound eyes composed of units called ommatidia (ommatidium, singular), possibly up to 30,000 in a single compound eye of, for example, large dragonflies. This type of eye gives less resolution than eyes found in vertebrates, but it gives acute perception of movement and usually possesses UV- and green sensitiity and may have additional sensitivity peaks in other regions of the visual spectrum. Often an ability to detect the E-vector of polarized light exists polarization of light.[11] There can also be an additional two or three ocelli, which help detect low light or small changes in light intensity. The image perceived is a combination of inputs from the numerous ommatidia, located on a convex surface, thus pointing in slightly different directions. Compared with simple eyes, compound eyes possess very large view angles and better acuity than the insect's dorsal ocelli, but some stemmatal (= larval eyes), for example those of sawfly larvae (Tenthredinidae) with an acuity 4 degrees and very high polarization sensitivity, match the performance of compound eyes.[12] [13]



Ocellus cross-section



Compound eye cross-section

Because the individual lenses are so small, the effects of diffraction impose a limit on the possible resolution that can be obtained (assuming they do not function as phased arrays). This can only be countered by increasing lens size and number. To see with a resolution comparable to our simple eyes, humans would require compound eyes that would each reach the size of their heads. Compound eyes fall into two groups: apposition eyes, which form multiple inverted images, and superposition eyes, which form a single erect image.[14][15] Compound eyes grow at their margins by the addition of new ommatidia.[16]

Antennae

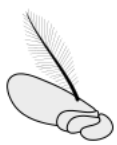
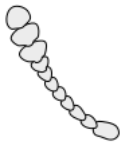
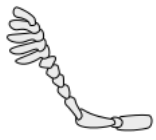
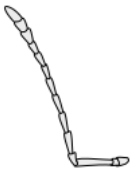
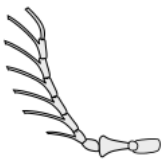
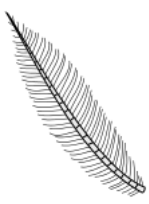
Antennae, sometimes called "feelers", are flexible appendages located on the insect's head which are used for sensing the environment. Insects *are* able to feel with their antennae because of the fine hairs (setae) that cover them.[17]:8–11 However, touch is not the only thing that antennae can detect; numerous tiny sensory structures on the antennae allow insects to sense smells, temperature, humidity, pressure, and even potentially sense themselves in space.[17]:8–11[18][19] Some insects, including bees and some groups of flies can also detect sound with their antennae.[20]

The number of segments in an antenna varies considerably amongst insects, with higher flies having only 3-6 segments,[21] while adult cockroaches can have over 140.[22] The general shape of the antennae is also quite variable, but the first segment (the one attached to the head) is always called the scape, and the second segment is called the pedicel. The remaining antennal segments or flagellomeres are called the flagellum.[17]:8–11

General insect antenna types are shown below:

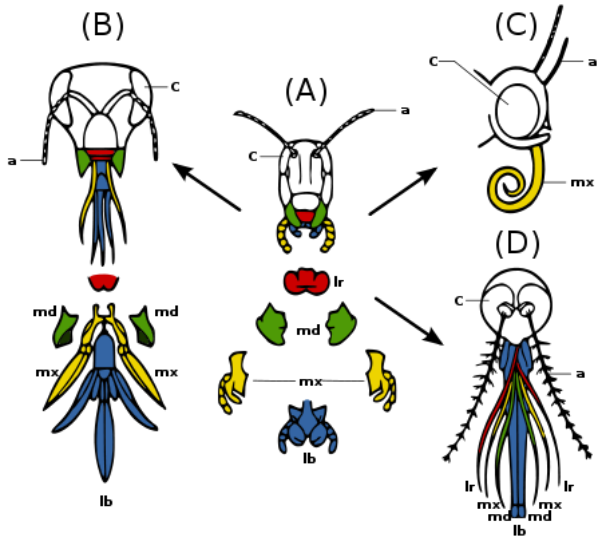

Closeup of a fire ant, showing fine sensory hairs on antennae

Types of insect antennae[1][17]:8–11

 **Aristate**	 **Capitate**	 **Clavate**	 **Filiform**	 **Flabellate**	 **Geniculate**	
 **Lamellate**	 **Moniliform**	 **Pectinate**	 **Plumose**	 **Serrate**	 **Stylate**	

Mouthparts

The insect mouthparts consist of the maxilla, labium, and in some species, the mandibles.[8]:16[23] The labrum is a simple, fused sclerite, often called the upper lip, and moves longitudinally, which is hinged to the clypeus. The mandibles (jaws) are a highly sclerotized pair of structures that move at right angles to the body, used for biting, chewing, and severing food. The maxillae are paired structures that can also move at right angles to the body and possess segmented palps. The labium (lower lip) is the fused structure that moves longitudinally and possesses a pair of segmented palps.[24]



The development of insect mouthparts from the primitive chewing mouthparts of a grasshopper in the centre (A), to the lapping type (B) of a bee, the siphoning type (C) of a butterfly and the sucking type (D) of a female mosquito.
Legend: a - antennae
c - compound eye
lb - labium
lr - labrum
md - mandibles
mx - maxillae

The mouthparts, along with the rest of the head, can be articulated in at least three different positions: prognathous, opisthognathous, and hypognathous. In species with prognathous articulation, the head is positioned vertically aligned with the body, such as species of Formicidae; while in a hypognathous type, the head is aligned horizontally adjacent to the body. An opisthognathous head is positioned diagonally, such as species of Blattodea and some Coleoptera.[25] The mouthparts vary greatly between insects of different orders, but the two main functional groups are mandibulate and haustellate. Haustellate mouthparts are used for sucking liquids and can be further classified by the presence of stylets, which include piercing-sucking, sponging, and siphoning. The stylets are needle-like projections used to penetrate plant and animal tissues. The stylets and the feeding tube form the modified mandibles, maxilla, and hypopharynx.[24]

- **Mandibulate** mouthparts, among the most common in insects, are used for biting and grinding solid foods.
- **Piercing-sucking** mouthparts have stylets, and are used to penetrate solid tissue and then suck up liquid food.
- **Sponging** mouthparts are used to sponge and suck liquids, and lack stylets (e.g. most Diptera).
- **Siphoning** mouthparts lack stylets and are used to suck liquids, and are commonly found among species of Lepidoptera.

Mandibular mouthparts are found in species of Odonata, adult Neuroptera, Coleoptera, Hymenoptera, Blattodea, Orthoptera, and Lepidoptera. However, most adult Lepidoptera have siphoning mouthparts, while their larvae (commonly called caterpillars) have mandibles.

Mandibulate

The labrum is a broad lobe forming the roof of the preoral cavity, suspended from the clypeus in front of the mouth and forming the upper lip.[1]:22–24 On its inner side, it is membranous and may be produced into a median lobe, the epipharynx, bearing some sensilla. The labrum is raised away from the mandibles by two muscles arising in the head and inserted medially into the anterior margin of the labrum. It is closed against the mandibles in part by two muscles arising in the head and inserted on the posterior lateral margins on two small sclerites, the tormae, and, at least in some insects, by a resilin spring in the cuticle at the junction of the labrum with the clypeus. [26] Until recently, the labrum generally was considered to be associated with first head segment. However, recent studies of the embryology, gene expression, and nerve supply to the labrum show it is innervated by the tritocerebrum of the brain, which is the fused ganglia of the third head segment. This is formed from fusion of parts of a pair of ancestral appendages found on the third head segment, showing their relationship.[1]:22–24 Its ventral, or inner, surface is usually membranous and forms the lobe-like epipharynx, which bears mechanosensilla and chemosensilla.[27][28]

Chewing insects have two mandibles, one on each side of the head. The mandibles are positioned between the labrum and maxillae. The mandibles cut and crush food, and may be used for defense; generally, they have an apical cutting edge, and the more basal molar area grinds the food. They can be extremely hard (around 3 on Mohs, or an indentation hardness of about 30 kg/mm^2); thus, many termites and beetles have no physical difficulty in boring through foils made from such common metals as copper, lead, tin, and zinc.[1]:22–24 The cutting edges are typically strengthened by the addition of zinc, manganese, or rarely, iron, in amounts up to about 4% of the dry weight.[27] They are typically the largest mouthparts of chewing insects, being used to masticate (cut, tear, crush, chew) food items. They open outwards (to the sides of the head) and come together medially. In carnivorous, chewing insects, the mandibles can be modified to be more knife-like, whereas in herbivorous chewing insects, they are more typically broad and flat on their opposing faces (e.g., caterpillars). In male stag beetles, the mandibles are modified to such an extent as to not serve any feeding function, but are instead are used to defend mating sites from other males. In ants, the mandibles also serve a defensive function (particularly in soldier castes). In bull ants, the mandibles are elongated and toothed, used as hunting (and defensive) appendages.

Situated beneath the mandibles, paired maxillae manipulate food during mastication. Maxillae can have hairs and "teeth" along their inner margins. At the outer margin, the galea is a cupped or scoop-like structure, which sits over the outer edge of the labium. They also have palps, which are used to sense the characteristics of potential foods. The maxillae occupy a lateral position, one on each side of the head behind the mandibles. The proximal part of the maxilla consists of a basal cardo, which has a single articulation with the head, and a flat plate, the stipes, hinged to the cardo. Both cardo and stipes are loosely joined to the head by membrane so they are capable of movement. Distally on the stipes are two lobes, an inner lacinea and an outer galea, one or both of which may be absent. More laterally on the stipes is a jointed, leglike palp made up of a number of segments; in Orthoptera there are five. Anterior and posterior rotator muscles are inserted on the cardo,

and ventral adductor muscles arising on the tentorium are inserted on both cardo and stipes. Arising in the stipes are flexor muscles of lacinea and galea and another lacineal flexor arises in the cranium, but neither the lacinea nor the galea has an extensor muscle. The palp has levator and depressor muscles arising in the stipes, and each segment of the palp has a single muscle causing flexion of the next segment.[26]

In mandibulate mouthparts, the labium is a quadrupedal structure, although it is formed from two fused secondary maxillae. It can be described as the floor of the mouth. With the maxillae, it assists with manipulation of food during mastication or chewing or, in the unusual case of the dragonfly nymph, extends out to snatch prey back to the head, where the mandibles can eat it. The labium is similar in structure to the maxilla, but with the appendages of the two sides fused by the midline, so they come to form a median plate. The basal part of the labium, equivalent to the maxillary cardines and possibly including a part of the sternum of the labial segment, is called the postmentum. This may be subdivided into a proximal submentum and a distal mentum. Distal to the postmentum, and equivalent to the fused maxillary stipites, is the prementum. The prementum closes the preoral cavity from behind. Terminally, it bears four lobes, two inner glossae, and two outer paraglossae, which are collectively known as the ligula. One or both pairs of lobes may be absent or they may be fused to form a single median process. A palp arises from each side of the prementum, often being three-segmented.[26]

The hypopharynx is a median lobe immediately behind the mouth, projecting forwards from the back of the preoral cavity; it is a lobe of uncertain origin, but perhaps associated with the mandibular segment;[26] in apterygotes, earwigs, and nymphal mayflies, the hypopharynx bears a pair of lateral lobes, the superlinguae (singular: superlingua). It divides the cavity into a dorsal food pouch, or cibarium, and a ventral salivarium into which the salivary duct opens.[1]:22–24 It is commonly found fused to the libium.[27] Most of the hypopharynx is membranous, but the adoral face is sclerotized distally, and proximally contains a pair of suspensory sclerites extending upwards to end in the lateral wall of the stomodeum. Muscles arising on the frons are inserted into these sclerites, which distally are hinged to a pair of lingual sclerites. These, in turn, have inserted into them antagonistic pairs of muscles arising on the tentorium and labium. The various muscles serve to swing the hypopharynx forwards and back, and in the cockroach, two more muscles run across the hypopharynx and dilate the salivary orifice and expand the salivarium.[26]

Examples of mandibles









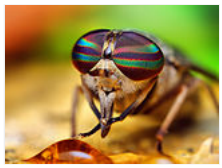
Piercing-sucking

Mouthparts can have multiple functions. Some insects combine piercing parts along with sponging ones which are then used to pierce through tissues of plants and animals. Female mosquitoes feed on blood (hemophagous) making them disease vectors. The mosquito mouthparts consist of the proboscis, paired mandibles and maxillae. The maxillae form needle-like structures, called stylets, which are enclosed by the labium. When mosquito bites, maxillae penetrate the skin and anchor the mouthparts, thus allowing other parts to be inserted. The sheath-like labium slides back, and the remaining mouthparts pass through its tip and into the tissue. Then, through the hypopharynx, the mosquito injects saliva, which contains anticoagulants to stop the blood from clotting. And finally, the labrum (upper lip) is used to suck up the blood. Species of the genus *Anopheles* are characterized by their long palpi (two parts with widening end), almost reaching the end of labrum.[29]

Examples of piercing mouthparts







Aedes aegypti | Mosquito | *Cimex lectularius* | Flea | Horsefly (female)



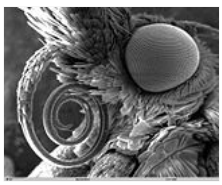
Tick (*Ixodes ricinus*), which is not an insect, but an arachnid, given for comparison

Siphoning

The proboscis is formed from maxillary galeae and is adaption found in some insects for sucking.[30] The muscles of the cibarium or pharynx are strongly developed and form the pump. In Hemiptera and many Diptera, which feed on fluids within plants or animals, some components of the mouthparts are modified for piercing, and the elongated structures are called stylets. The combined tubular structures are referred to as the proboscis, although specialized terminology is used in some groups.

In species of Lepidoptera, it consists of two tubes held together by hooks and separable for cleaning. Each tube is inwardly concave, thus forming a central tube through which moisture is sucked. Suction is effected through the contraction and expansion of a sac in the head.[31] The proboscis is coiled under the head when the insect is at rest, and is extended only when feeding.[30] The maxillary palpi are reduced or even vestigial.[32] They are conspicuous and five-segmented in some of the more basal families, and are often folded.[8] The shape and dimensions of the proboscis have evolved to give different species wider and therefore more advantageous diets.[30] There is an allometric scaling relationship between body mass of Lepidoptera and length of proboscis[33] from which an interesting adaptive departure is the unusually long-tongued hawk moth *Xanthopan morganii praedicta*. Charles Darwin predicted the existence and proboscis length of this moth before its discovery based on his knowledge of the long-spurred Madagascan star orchid *Angraecum sesquipedale*.[34]

Examples of siphoning mouthparts






Sponging

The mouthparts of insects that feed on fluids are modified in various ways to form a tube through which liquid can be drawn into the mouth and usually another through which saliva passes. The muscles of the cibarium or pharynx are strongly developed to form a pump.[26] In nonbiting flies, the mandibles are absent and other structures are reduced; the labial palps have become modified to form the labellum, and the maxillary palps are present, although sometimes short. In Brachycera, the labellum is especially prominent and used for sponging liquid or semiliquid food.[35] The labella are a complex structure consisting of many grooves, called pseudotracheae, which sop up liquids. Salivary secretions from the labella assist in dissolving and collecting food particles so they can be more easily taken up by the pseudotracheae; this is thought to occur by capillary action. The liquid food is then drawn up from the pseudotracheae through the food channel into the esophagus.[36]

The mouthparts of bees are of a chewing and lapping-sucking type. Lapping is a mode of feeding in which liquid or semiliquid food adhering to a protrusible organ, or "tongue", is transferred from substrate to mouth. In the honey bee (Hymenoptera: Apidae: *Apis mellifera*), the elongated and fused labial glossae form a hairy tongue, which is surrounded by the maxillary galeae and the labial palps to form a tubular proboscis containing a food canal. In feeding, the tongue is dipped into the nectar or honey, which adheres to the hairs, and then is retracted so the adhering liquid is carried into the space between the galeae and labial palps. This back-and-forth glossal movement occurs repeatedly. Movement of liquid to the mouth apparently results from the action of the cibarial pump, facilitated by each retraction of the tongue pushing liquid up the food canal.[1]:22–24

Examples of sponging mouthparts




Thorax

The insect thorax has three segments: the prothorax, mesothorax, and metathorax. The anterior segment, closest to the head, is the prothorax; its major features are the first pair of legs and the pronotum. The middle segment is the mesothorax; its major features are the second pair of legs and the anterior wings, if any. The third, the posterior, thoracic segment, abutting the abdomen, is the metathorax, which bears the third pair of legs and the posterior wings. Each segment is dilineated by an intersegmental suture. Each segment has four basic regions. The dorsal surface is called the

tergum (or notum, to distinguish it from the abdominal terga).[1]:22–24 The two lateral regions are called the pleura (singular: pleuron), and the ventral aspect is called the sternum. In turn, the notum of the prothorax is called the pronotum, the notum for the mesothorax is called the mesonotum and the notum for the metathorax is called the metanotum. Continuing with this logic, there is also the mesopleura and metapleura, as well as the mesosternum and metasternum.[8]

The tergal plates of the thorax are simple structures in apterygotes and in many immature insects, but are variously modified in winged adults. The pterothoracic nota each have two main divisions: the anterior, wing-bearing alinotum and the posterior, phragma-bearing postnotum. Phragmata (singular: phragma) are plate-like apodemes that extend inwards below the antecostal sutures, marking the primary intersegmental folds between segments; phragmata provide attachment for the longitudinal flight muscles. Each alinotum (sometimes confusingly referred to as a "notum") may be traversed by sutures that mark the position of internal strengthening ridges, and commonly divides the plate into three areas: the anterior prescutum, the scutum, and the smaller posterior scutellum. The lateral pleural sclerites are believed to be derived from the subcoxal segment of the ancestral insect leg. These sclerites may be separate, as in silverfish, or fused into an almost continuous sclerotic area, as in most winged insects.[1]:22–24

Prothorax

The pronotum of the prothorax may be simple in structure and small in comparison with the other nota, but in beetles, mantids, many bugs, and some Orthoptera, the pronotum is expanded, and in cockroaches, it forms a shield that covers part of the head and mesothorax.[8][1]:22–24

Pterothorax

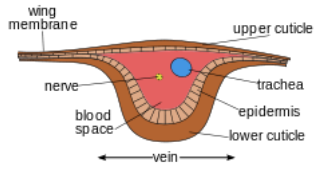
Because the mesothorax and metathorax hold the wings, they have a combined name called the pterothorax (pteron = wing). The forewing, which goes by different names in different orders (e.g., the tegmina in Orthoptera and elytra in Coleoptera), arises between the mesonotum and the mesopleuron, and the hindwing articulates between the metanotum and metapleuron. The legs arise from the mesopleuron and metapleura. The mesothorax and metathorax each have a pleural suture (mesopleural and metapleural sutures) that runs from the wing base to the coxa of the leg. The sclerite anterior to the pleural suture is called the episternum (serially, the mesepisternum and metepisternum). The sclerite posterior to the suture is called the epimiron (serially, the mesepimiron and metepimiron). Spiracles, the external organs of the respiratory system, are found on the pterothorax, usually one between the pro- and mesopleoron, as well as one between the meso- and metapleuron.[8]

The ventral view or sternum follows the same convention, with the prosternum under the prothorax, the mesosternum under the mesothorax and the metasternum under the metathorax. The notum, pleura, and sternum of each segment have a variety of different sclerites and sutures, varying greatly from order to order, and they will not be discussed in detail in this section.[8]

Wings

Most phylogenetically advanced insects have two pairs of wings located on the second and third thoracic segments.[1]:22–24 Insects are the only invertebrates to have developed flight capability, and this has played an important part in their success. Insect flight is not very well understood, relying heavily on turbulent aerodynamic effects. The primitive insect groups use muscles that act directly on the wing structure. The more advanced groups making up the Neoptera have foldable wings, and their muscles act on the thorax wall and power the wings indirectly.[1]:22–24 These muscles are able to contract multiple times for each single nerve impulse, allowing the wings to beat faster than would ordinarily be possible.

Insect flight can be extremely fast, maneuverable, and versatile, possibly due to the changing shape, extraordinary control, and variable motion of the insect wing. Insect orders use different flight mechanisms; for example, the flight of a butterfly can be explained using steady-state, nontransitory aerodynamics, and thin airfoil theory.

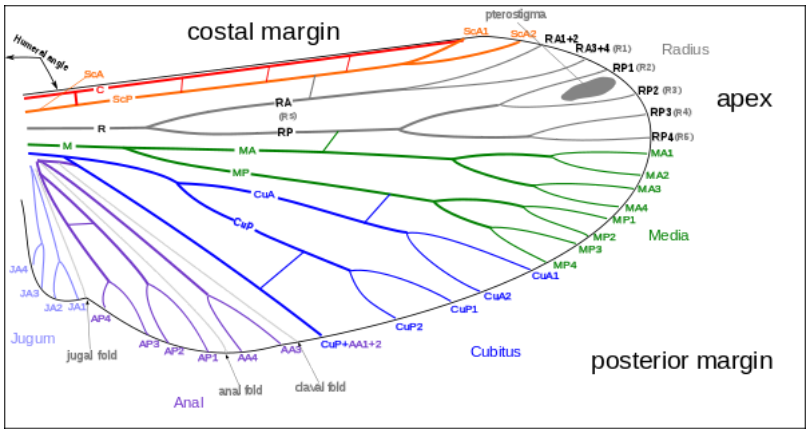


Internal

Each of the wings consists of a thin membrane supported by a system of veins. The membrane is formed by two layers of integument closely apposed, while the veins are formed where the two layers remain separate and the cuticle may be thicker and more heavily sclerotized. Within each of the major veins is a nerve and a trachea, and, since the cavities of the veins are connected with the hemocoel, hemolymph can flow into the wings.[26] Also, the wing lumen, being an extension of the hemocoel, contains the tracheae, nerves, and hemolymph. As the wing develops, the dorsal and ventral integumental layers become closely apposed over most of their area, forming the wing membrane. The remaining areas form channels, the future veins, in which the nerves and tracheae may occur. The cuticle surrounding the veins becomes thickened and more heavily sclerotized to provide strength and rigidity to the wing. Hairs of two types may occur on the wings: microtrichia, which are small and irregularly scattered, and macrotrichia, which are larger, socketed, and may be restricted to veins. The scales of Lepidoptera and Trichoptera are highly modified macrotrichia.[27]

Veins

In some very small insects, the venation may be greatly reduced. In chalcid wasps, for instance, only the subcosta and part of the radius are present. Conversely, an increase in venation may occur by the branching of existing veins to produce accessory veins or by the development of additional, intercalary veins between the original ones, as in the wings of Orthoptera (grasshoppers and crickets). Large numbers of cross-veins are present in some insects, and they may form a reticulum as in the wings of Odonata (dragonflies and damselflies) and at the base of the forewings of Tettigonioidea and Acridoidea (katydids and grasshoppers, respectively).[26]



Venation of insect wings, based on the Comstock-Needham system

The archedictyon is the name given to a hypothetical scheme of wing venation proposed for the very first winged insect. It is based on a combination of speculation and fossil data. Since all winged insects are believed to have evolved from a common ancestor, the archediction represents the "template" that has been modified (and streamlined) by natural selection for 200 million years. According to current dogma, the archedictyon contained six to eight longitudinal veins. These veins (and their branches) are named according to a system devised by John Comstock and George Needham—the Comstock-Needham system:[37]

- **Costa (C)** - the leading edge of the wing
- **Subcosta (Sc)** - second longitudinal vein (behind the costa), typically unbranched

- **Radius (R)** - third longitudinal vein, one to five branches reach the wing margin
- **Media (M)** - fourth longitudinal vein, one to four branches reach the wing margin
- **Cubitus (Cu)** - fifth longitudinal vein, one to three branches reach the wing margin
- **Anal veins (A1, A2, A3)** - unbranched veins behind the cubitus

The costa (C) is the leading marginal vein on most insects, although a small vein, the precosta, is sometimes found above the costa. In almost all extant insects,[1]:41–42 the precosta is fused with the costa; the costa rarely ever branches because it is at the leading edge, which is associated at its base with the humeral plate. The trachea of the costal vein is perhaps a branch of the subcostal trachea. Located after the costa is the third vein, the subcosta, which branches into two separate veins: the anterior and posterior. The base of the subcosta is associated with the distal end of the neck of the first axillary. The fourth vein is the radius, which is branched into five separate veins. The radius is generally the strongest vein of the wing. Toward the middle of the wing, it forks into a first undivided branch (R1) and a second branch, called the radial sector (Ra), which subdivides dichotomously into four distal branches (R2, R3, R4, R5). Basally, the radius is flexibly united with the anterior end of the second axillary (2Ax).[38]

The fifth vein of the wing is the media. In the archetype pattern (A), the media forks into two main branches, a media anterior (MA), which divides into two distal branches (MA1, MA2), and a median sector, or media posterior (MP), which has four terminal branches (M1, M2, M3, M4). In most modern insects, the media anterior has been lost, and the usual "media" is the four-branched media posterior with the common basal stem. In the Ephemerida, according to present interpretations of the wing venation, both branches of the media are retained, while in Odonata, the persisting media is the primitive anterior branch. The stem of the media is often united with the radius, but when it occurs as a distinct vein, its base is associated with the distal median plate (m') or is continuously sclerotized with the latter. The cubitus, the sixth vein of the wing, is primarily two-branched. The primary forking takes place near the base of the wing, forming the two principal branches (Cu1, Cu2). The anterior branch may break up into a number of secondary branches, but commonly it forks into two distal branches. The second branch of the cubitus (Cu2) in Hymenoptera, Trichoptera, and Lepidoptera, was mistaken by Comstock and Needham for the first anal. Proximally, the main stem of the cubitus is associated with the distal median plate (m') of the wing base.[38]

The postcubitus (Pcu) is the first anal of the Comstock and Needham system. The postcubitus, however, has the status of an independent wing vein and should be recognized as such. In nymphal wings, its trachea arises between the cubital trachea and the group of vannal tracheae. In the mature wings of more generalized insects, the postcubitus is always associated proximally with the cubitus, and is never intimately connected with the flexor sclerite (3Ax) of the wing base. In Neuroptera, Mecoptera, and Trichoptera, the postcubitus may be more closely associated with the vannal veins, but its base is always free from the latter. The postcubitus is usually unbranched; primitively, it is two-branched. The vannal veins (lV to nV) are the anal veins immediately associated with the third axillary, and which are directly affected by the movement of this sclerite that brings about the flexion of the wings. In number, the vannal veins vary from one to 12, according to the expansion of the vannal area of the wing. The vannal tracheae usually arise from a common tracheal stem in nymphal insects, and the veins are regarded as branches of a single anal vein. Distally, the vannal veins are either simple or branched. The jugal vein (J) of the jugal lobe of the wing is often occupied by a network of irregular veins, or it may be entirely membranous; sometimes it contains one or two distinct, small veins, the first jugal vein, or vena arcuata, and the second jugal vein, or vena cardinalis (2J).[38]

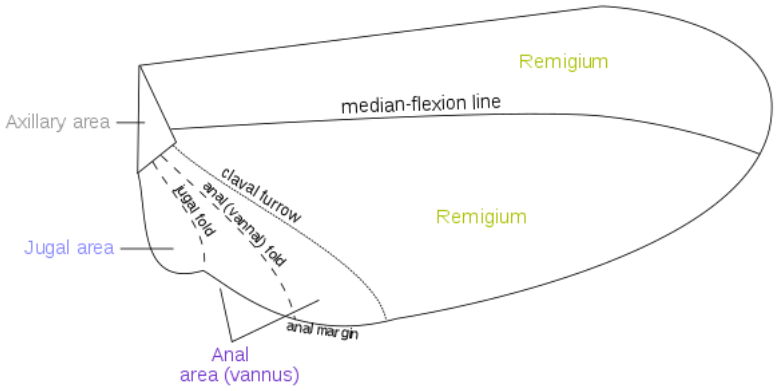
- **C-Sc cross-veins** - run between the costa and subcosta
- **R cross-veins** - run between adjacent branches of the radius
- **R-M cross-veins** - run between the radius and media
- **M-Cu cross-veins** - run between the media and cubitus

All the veins of the wing are subject to secondary forking and to union by cross-veins. In some orders of insects, the cross-veins are so numerous, the whole venational pattern becomes a close network of branching veins and cross-veins. Ordinarily, however, a definite number of cross-veins having specific locations occurs. The more constant cross-veins are the humeral cross-vein (h) between the costa and subcosta, the radial cross-vein (r) between R and the first fork of Rs, the sectorial cross-vein (s) between the two forks of R8, the median cross-vein (m-m) between M2 and M3, and the mediocubital cross-vein (m-cu) between the media and the cubitus.[38]

The veins of insect wings are characterized by a convex-concave placement, such as those seen in mayflies (i.e., concave is "down" and convex is "up"), which alternate regularly and by their branching; whenever a vein forks there is always an interpolated vein of the opposite position between the two branches. The concave vein will fork into two concave veins (with the interpolated vein being convex) and the regular alteration of the veins is preserved.[39] The veins of the wing appear to fall into an undulating pattern according to whether they have a tendency to fold up or down when the wing is relaxed. The basal shafts of the veins are convex, but each vein forks distally into an anterior convex branch and a posterior concave branch. Thus, the costa and subcosta are regarded as convex and concave branches of a primary first vein, Rs is the concave branch of the radius, posterior media the concave branch of the media, Cu1 and Cu2 are respectively convex and concave, while the primitive postcubitus and the first vannal have each an anterior convex branch and a posterior concave branch. The convex or concave nature of the veins has been used as evidence in determining the identities of the persisting distal branches of the veins of modern insects, but it has not been demonstrated to be consistent for all wings.[26][38]

Fields

Wing areas are delimited and subdivided by fold lines, along which the wings can fold, and flexion lines, which flex during flight. Between the flexion and the fold lines, the fundamental distinction is often blurred, as fold lines may permit some flexibility or vice versa. Two constants, found in nearly all insect wings, are the claval (a flexion line) and jugal folds (or fold line), forming variable and unsatisfactory boundaries. Wing foldings can very complicated, with transverse folding occurring in the hindwings of Dermaptera and Coleoptera, and in some insects, the anal area can be folded like a fan.[1]:41–42 The four different fields found on insect wings are:



- **Remigium**
- **Anal area (vannus)**
- **Jugal area**
- **Axillary area**
- **Alula**

Most veins and cross-veins occur in the anterior area of the remigium, which is responsible for most of the flight, powered by the thoracic muscles. The posterior portion of the remigium is sometimes called the clavus; the two other posterior fields are the anal and jugal areas.[1]:41–42 When the vannal fold has the usual position anterior to the group of anal veins, the remigium contains the costal, subcostal, radial, medial, cubital, and postcubital veins. In the flexed wing, the remigium turns posteriorly on the flexible basal connection of the radius with the second axillary, and the base of the mediocubital field is folded medially on the axillary region along the plica basalis (bf) between the median plates (m, m') of the wing base.[38]

The vannus is bordered by the vannal fold, which typically occurs between the postcubitus and the first vannal vein. In Orthoptera, it usually has this position. In the forewing of Blattidae, however, the only fold in this part of the wing lies immediately before the postcubitus. In Plecoptera, the vannal fold is posterior to the postcubitus, but proximally it crosses the base of the first vannal vein. In the cicada, the vannal fold lies immediately behind the first vannal vein (lV). These small variations in the actual position of the vannal fold, however, do not affect the unity of action of the vannal veins, controlled by the flexor sclerite (3Ax), in the flexion of the wing. In the hindwings of most Orthoptera, a secondary vena dividens forms a rib in the vannal fold. The vannus is usually

triangular in shape, and its veins typically spread out from the third axillary like the ribs of a fan. Some of the vannal veins may be branched, and secondary veins may alternate with the primary veins. The vannal region is usually best developed in the hindwing, in which it may be enlarged to form a sustaining surface, as in Plecoptera and Orthoptera. The great fan-like expansions of the hindwings of Acrididae are clearly the vannal regions, since their veins are all supported on the third axillary sclerites on the wing bases, though Martynov (1925) ascribes most of the fan areas in Acrididae to the jugal regions of the wings. The true jugum of the acridid wing is represented only by the small membrane (Ju) mesad of the last vannal vein. The jugum is more highly developed in some other Orthoptera, as in the Mantidae. In most of the higher insects with narrow wings, the vannus becomes reduced, and the vannal fold is lost, but even in such cases, the flexed wing may bend along a line between the postcubitus and the first vannal vein.[38]

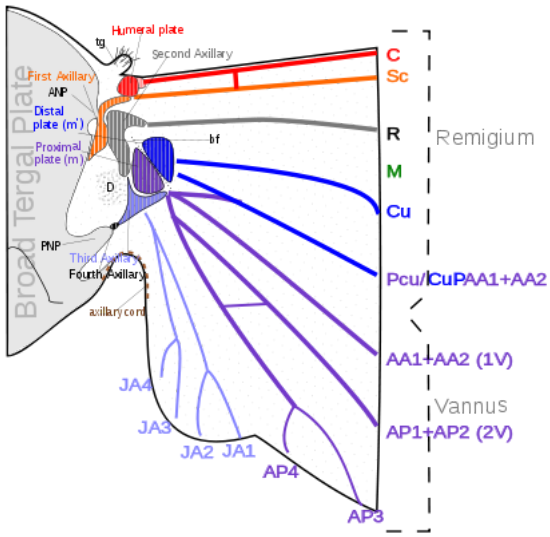
The jugal region, or neala, is a region of the wing that is usually a small membranous area proximal to the base of the vannus strengthened by a few small, irregular vein-like thickenings; but when well developed, it is a distinct section of the wing and may contain one or two jugal veins. When the jugal area of the forewing is developed as a free lobe, it projects beneath the humeral angle of the hindwing and thus serves to yoke the two wings together. In the Jugatae group of Lepidoptera, it bears a long finger-like lobe. The jugal region was termed the neala ("new wing") because it is evidently a secondary and recently developed part of the wing.[38]

The auxiliary region containing the axillary sclerites has, in general, the form of a scalene triangle. The base of the triangle (a-b) is the hinge of the wing with the body; the apex (c) is the distal end of the third axillary sclerite; the longer side is anterior to the apex. The point d on the anterior side of the triangle marks the articulation of the radial vein with the second axillary sclerite. The line between d and c is the plica basalis (bf), or fold of the wing at the base of the mediocubital field.[38]

At the posterior angle of the wing base in some Diptera there is a pair of membranous lobes (squamae, or calypteres) known as the alula. The alula is well developed in the house fly. The outer squama (c) arises from the wing base behind the third axillary sclerite (3Ax) and evidently represents the jugal lobe of other insects (A, D); the larger inner squama (d) arises from the posterior scutellar margin of the tergum of the wing-bearing segment and forms a protective, hood-like canopy over the halter. In the flexed wing, the outer squama of the alula is turned upside down above the inner squama, the latter not being affected by the movement of the wing. In many Diptera, a deep incision of the anal area of the wing membrane behind the single vannal vein sets off a proximal alar lobe distal to the outer squama of the alula.[38]

Joints

The various movements of the wings, especially in insects that flex their wings horizontally over their backs when at rest, demand a more complicated articular structure at the wing base than a mere hinge of the wing with the body. Each wing is attached to the body by a membranous basal area, but the articular membrane contains a number of small articular sclerites, collectively known as the pteralia. The pteralia include an anterior humeral plate at the base of the costal vein, a group of axillaries (Ax) associated with the subcostal, radial, and vannal veins, and two less definite median plates (m, m') at the base of the mediocubital area. The axillaries are specifically developed only in the wing-flexing insects, where they constitute the flexor mechanism of the wing operated by the flexor muscle arising on the pleuron. Characteristic of the wing base is also a small lobe on the anterior margin of the articular area proximal to the humeral plate, which, in the forewing of some insects, is developed into a large, flat, scale-like flap, the tegula, overlapping the base of the wing. Posteriorly, the articular membrane often forms an ample lobe between the wing and the body, and its margin is generally thickened and corrugated, giving the appearance of a ligament, the so-called axillary cord, continuous mesally with the posterior marginal scutellar fold of the tergal plate bearing the wing.[38]



The articular sclerites, or pteralia, of the wing base of the wing-flexing insects and their relations to the body and the wing veins, shown diagrammatically, are as follows:

- **Humeral plates**
- **First Axillary**
- **Second Axillary**
- **Third Axillary**
- **Fourth Axillary**
- **Median plates (m, m')**

The humeral plate is usually a small sclerite on the anterior margin of the wing base, movable and articulated with the base of the costal vein. Odonata have their humeral plates greatly enlargened,[38] with two muscles arising from the episternum inserted into the humeral plates and two from the edge of the epimeron inserted into the axillary plate.[26]

The first axillary sclerite (lAx) is the anterior hinge plate of the wing base. Its anterior part is supported on the anterior notal wing process of the tergum (ANP); its posterior part articulates with the tergal margin. The anterior end of the sclerite is generally produced as a slender arm, the apex of which (e) is always associated with the base of the subcostal vein (Sc), though it is not united with the latter. The body of the sclerite articulates laterally with the second axillary. The second axillary sclerite (2Ax) is more variable in form than the first axillary, but its mechanical relations are no less definite. It is obliquely hinged to the outer margin of the body of the first axillary, and the radial vein (R) is always flexibly attached to its anterior end (d). The second axillary presents both a dorsal and a ventral sclerotization in the wing base; its ventral surface rests upon the fulcral wing process of the pleuron. The second axillary, therefore, is the pivotal sclerite of the wing base, and it specifically manipulates the radial vein.[38]

The third axillary sclerite (3Ax) lies in the posterior part of the articular region of the wing. Its form is highly variable and often irregular, but the third axillary is the sclerite on which is inserted the flexor muscle of the wing (D). Mesally, it articulates anteriorly (f) with the posterior end of the second axillary, and posteriorly (b) with the posterior wing process of the tergum (PNP), or with a small fourth axillary when the latter is present. Distally, the third axillary is prolonged in a process always associated with the bases of the group of veins in the anal region of the wing, here termed the vannal veins (V). The third axillary, therefore, is usually the posterior hinge plate of the wing base and is the active sclerite of the flexor mechanism, which directly manipulates the vannal veins. The contraction of the flexor muscle (D) revolves the third axillary on its mesal articulations (b, f), and thereby lifts its distal arm; this movement produces the flexion of the wing. The fourth axillary sclerite is not a constant element of the wing base. When present, it is usually a small plate intervening between the third axillary and the posterior notal wing process, and is probably a detached piece of the latter.[38]

The median plates (m, m') are also sclerites that are not so definitely differentiated as specific plates as are the three principal axillaries, but they are important elements of the flexor apparatus. They lie in the median area of the wing base distal to the second and third axillaries, and are separated from each other by an oblique line (bf), which forms a prominent convex fold during flexion of the wing. The proximal plate (m) is usually attached to the distal arm of the third axillary and perhaps should be regarded as a part of the latter. The distal plate (m') is less constantly present as a distinct sclerite, and may be represented by a general sclerotization of the base of the mediocubital field of the wing. When the veins of this region are distinct at their bases, they are associated with the outer median plate.[38]

Coupling, folding, and other features

In many insect species, the forewing and hindwing are coupled together, which improves the aerodynamic efficiency of flight. The most common coupling mechanism (e.g., Hymenoptera and Trichoptera) is a row of small hooks on the forward margin of the hindwing, or "hamuli", which lock onto the forewing, keeping them held together (hamulate coupling). In some other insect species (e.g., Mecoptera, Lepidoptera, and some Trichoptera) the jugal lobe of the forewing covers a portion of the hindwing (jugal coupling), or the margins of the forewing and hindwing overlap broadly (amplexiform coupling), or the hindwing bristles, or frenulum, hook under the retaining structure or retinalucum on the forewing.[1]:43

When at rest, the wings are held over the back in most insects, which may involve longitudinal folding of the wing membrane and sometimes also transverse folding. Folding may sometimes occur along the flexion lines. Though fold lines may be transverse, as in the hindwings of beetles and earwigs, they are normally radial to the base of the wing, allowing adjacent sections of a wing to be folded over or under each other. The commonest fold line is the jugal fold, situated just behind the third anal vein,[27] although, most Neoptera have a jugal fold just behind vein 3A on the forewings. It is sometimes also present on the hindwings. Where the anal area of the hindwing is large, as in Orthoptera and Blattodea, the whole of this part may be folded under the anterior part of the wing along a vannal fold a little posterior to the claval furrow. In addition, in Orthoptera and Blattodea, the anal area is folded like a fan along the veins, the anal veins being convex, at the crests of the folds, and the accessory veins concave. Whereas the claval furrow and jugal fold are probably homologous in different species, the vannal fold varies in position in different taxa. Folding is produced by a muscle arising on the pleuron and inserted into the third axillary sclerite in such a waythat, when it contracts, the sclerite pivots about its points of articulation with the posterior notal process and the second axillary sclerite.[26]

As a result, the distal arm of the third axillary sclerite rotates upwards and inwards, so that finally its position is completely reversed. The anal veins are articulated with this sclerite in such a way that when it moves they are carried with it and become flexed over the back of the insect. Activity of the same muscle in flight affects the power output of the wing and so it is also important in flight control. In orthopteroid insects, the elasticity of the cuticle causes the vannal area of the wing to fold along the veins. Consequently, energy is expended in unfolding this region when the wings are moved to the flight position. In general, wing extension probably results from the contraction of muscles attached to the basalar sclerite or, in some insects, to the subalar sclerite.[26]

Legs

The typical and usual segments of the insect leg are divided into the coxa, one trochanter, the femur, the tibia, the tarsus, and the pretarsus. The coxa in its more symmetrical form, has the shape of a short cylinder or truncate cone, though commonly it is ovate and may be almost spherical. The proximal end of the coxa is girdled by a submarginal basicostal suture that forms internally a ridge, or basicosta, and sets off a marginal flange, the coxomarginale, or basicoxite. The basicosta strengthens the base of the coxa and is commonly enlarged on the outer wall to give insertion to muscles; on the mesal half of the coxa, however, it is usually weak and often confluent with the coxal margin. The trochanteral muscles that take their origin in the coxa are always attached distal to the basicosta. The coxa is attached to the body by an articular membrane, the coxal corium, which surrounds its base. These two articulations are perhaps the primary dorsal and ventral articular points of the subcoxo-coxal hinge. In addition, the insect coxa has often an anterior articulation with the anterior, ventral end of the trochantin, but the trochantinal articulation does not coexist with a sternal articulation. The pleural articular surface of the coxa is borne on a mesal inflection of the coxal wall. If the coxa is movable on the pleural articulation alone, the coxal articular surface is usually inflected to a sufficient depth to give a leverage to the abductor muscles inserted on the outer rim of the coxal base. Distally the coxa bears an anterior and a posterior articulation with the trochanter. The outer wall of the coxa is often marked by a suture extending from the base to the anterior trochanteral articulation. In some insects the coxal suture falls in line with the pleural suture, and in such cases the coxa appears to be divided into two parts corresponding to the episternum and epimeron of the pleuron. The coxal suture is absent in many insects.[38]:163–164

The inflection of the coxal wall bearing the pleural articular surface divides the lateral wall of the basicoxite into a prearticular part and a postarticular part, and the two areas often appear as two marginal lobes on the base of the coxa. The posterior lobe is usually the larger and is termed the meron. The meron may be greatly enlarged by an extension distally in the posterior wall of the coxa; in the Neuroptera, Mecoptera, Trichoptera, and Lepidoptera, the meron is so large that the coxa appears to be divided into an anterior piece, the so-called "coxa genuina," and the meron, but the meron never includes the region of the posterior trochanteral articulation, and the groove delimiting it is always a part of the basicostal suture. A coxa with an enlarged meron has an appearance similar to one divided by a coxal suture falling in line with the pleural suture, but the two conditions are fundamentally quite different and should not be confused. The meron reaches the extreme of its departure from the usual condition in the Diptera. In some of the more generalized flies, as in the Tipulidae, the meron of the middle leg appears as a large lobe of the coxa projecting upward and posteriorly from the coxal base; in higher members of the order it becomes completely separated from the coxa and forms a plate of the lateral wall of the mesothorax.[38]:164

The trochanter is the basal segment of the telopodite; it is always a small segment in the insect leg, freely movable by a horizontal hinge on the coxa, but more or less fixed to the base of the femur. When movable on the femur the trochantero femoral hinge is usually vertical or oblique in a vertical plane, giving a slight movement of production and reduction at the joint, though only a reductor muscle is present. In the Odonata, both nymphs and adults, there are two trochanteral segments, but they are not movable on each other; the second contains the reductor muscle of the femur. The usual single trochanteral segment of insects, therefore, probably represents the two trochanters of other arthropods fused into one apparent segment, since it is not likely that the primary coxotrochanteral hinge has been lost from the leg. In some of the Hymenoptera a basal subdivision of the femur simulates a second trochanter, but the insertion of the reductor muscle on its base attests that it belongs to the femoral segment, since as shown in the odonate leg, the reductor has its origin in the true second trochanter.[38]:165

The femur is the third segment of the insect leg, is usually the longest and strongest part of the limb, but it varies in size from the huge hind femur of leaping Orthoptera to a very small segment such as is present in many larval forms. The volume of the femur is generally correlated with the size of the tibial muscles contained within it, but it is sometimes enlarged and modified in shape for other purposes than that of accommodating the tibial muscles. The tibia is characteristically a slender segment in adult insects, only a little shorter than the femur or the combined femur and trochanter. Its proximal end forms a more or less distinct head bent toward the femur, a device allowing the tibia to be flexed close against the under surface of the femur.[38]:165

The terms profemur, mesofemur and metafemur refer to the femora of the front, middle and hind legs of an insect, respectively.[40] Similarly protibia, mesotibia and metatibia refer to the tibiae of the front, middle and hind legs.[41]

The tarsus of insects corresponds to the penultimate segment of a generalized arthropod limb, which is the segment called the propodite in Crustacea. adult insects it is commonly subdivided into from two to five subsegments, or tarsomeres, but in the Protura, some Collembola, and most holometabolous insect larvae it preserves the primitive form of a simple segment. The subsegments of the adult insect tarsus are usually freely movable on one another by inflected connecting membranes, but the tarsus never has intrinsic muscles. The tarsus of adult pterygote insects having fewer than five subsegments is probably specialized by the loss of one or more subsegments or by a fusion of adjoining subsegments. In the tarsi of Acrididae the long basal piece is evidently composed of three united tarsomeres, leaving the fourth and the fifth. The basal tarsomere is sometimes conspicuously enlarged and is distinguished as the basitarsus. On the under surfaces of the tarsal subsegments in certain Orthoptera there are small pads, the tarsal pulvilli, or euplantulae. The tarsus is occasionally fused with the tibia in larval insects, forming a tibiotarsal segment; in some cases it appears to be eliminated or reduced to a rudiment between the tibia and the pretarsus.[38]:165–166

For the most part the femur and tibia are the longest leg segments but variations in the lengths and robustness of each segment relate to their functions. For example, gressorial and cursorial, or walking and running type insects respectively, usually have well-developed femora and tibiae on all legs, whereas jumping (saltatorial) insects such as grasshoppers have disproportionately developed metafemora and metatibiae. In aquatic beetles (Coleoptera) and bugs (Hemiptera), the tibiae and/or tarsi of one or more pairs of legs usually are modified for swimming (natatorial) with fringes of long, slender hairs. Many ground-dwelling insects, such as mole crickets (Orthoptera: Gryllotalpidae), nymphal cicadas (Hemiptera: Cicadidae), and scarab beetles (Scarabaeidae), have the tibiae of the forelegs (protibiae) enlarged and modified for digging (fossorial), whereas the forelegs of some predatory insects, such as mantispid lacewings (Neuroptera) and mantids (Mantodea), are specialized for seizing prey, or raptorial. The tibia and basal tarsomere of each hindleg of honey bees are modified for the collection and carriage of pollen.[26]:45

Abdomen

The ground plan of the abdomen of an adult insect typically consists of 11–12 segments and is less strongly sclerotized than the head or thorax. Each segment of the abdomen is represented by a sclerotized tergum, sternum, and perhaps a pleurite. Terga are separated from each other and from the adjacent sterna or pleura by a membrane. Spiracles are located in the pleural area. Variation of this ground plan includes the fusion of terga or terga and sterna to form continuous dorsal or ventral shields or a conical tube. Some insects bear a sclerite in the pleural area called a laterotergite. Ventral sclerites are sometimes called laterosternites. During the embryonic stage of many insects and the postembryonic stage of primitive insects, 11 abdominal segments are present. In modern insects there is a tendency toward reduction in the number of the abdominal segments, but the primitive number of 11 is maintained during embryogenesis.Variation in abdominal segment number is considerable. If the Apterygota are considered to be indicative of the ground plan for pterygotes, confusion reigns: adult Protura have 12 segments, Collembola have 6. The orthopteran family Acrididae has 11 segments, and a fossil specimen of Zoraptera has a 10-segmented abdomen.[8]

Generally, the first seven abdominal segments of adults (the pregenital segments) are similar in structure and lack appendages. However, apterygotes (bristletails and silverfish) and many immature aquatic insects have abdominal appendages. Apterygotes possess a pair of styles; rudimentary appendages that are serially homologous with the distal part of the thoracic legs. And, mesally, one or two pairs of protrusible (or exsertile) vesicles on at least some abdominal segments. These vesicles are derived from the coxal and trochanteral endites (inner annulated lobes) of the ancestral abdominal appendages. Aquatic larvae and nymphs may have gills laterally on some to most abdominal segments.[1]:49 Of the rest of the abdominal segments consist of the reproductive and anal parts.

The anal-genital part of the abdomen, known as the terminalia, consists generally of segments 8 or 9 to the abdominal apex. Segments 8 and 9 bear the genitalia; segment 10 is visible as a complete segment in many "lower" insects but always lacks appendages; and the small segment 11 is represented by a dorsal epiproct and pair of ventral paraprocts derived from the sternum. A pair of appendages, the cerci, articulates laterally on segment 11; typically these are annulated and filamentous but have been modified (e.g. the forceps of earwigs) or reduced in different insect orders. An annulated caudal filament, the median appendix dorsalis, arises from the tip of the epiproct in apterygotes, most mayflies (Ephemeroptera), and a few fossil insects. A similar structure in nymphal stoneflies (Plecoptera) is of uncertain homology. These terminal abdominal segments have excretory and sensory functions in all insects, but in adults there is an additional reproductive function.[1]:49

External genitalia

The organs concerned specifically with mating and the deposition of eggs are known collectively as the external genitalia, although they may be largely internal. The components of the external genitalia of insects are very diverse in form and often have considerable taxonomic value, particularly among species that appear structurally similar in other respects. The male external genitalia have been used widely to aid in distinguishing species, whereas the female external genitalia may be simpler and less varied.



The abdominal terminus of male scorpionflies is enlarged into a "genital bulb", as seen in *Panorpa communis*

The terminalia of adult female insects include internal structures for receiving the male copulatory organ and his spermatozoa and external structures used for oviposition (egg-laying; section 5.8). Most female insects have an egg-laying tube, or ovipositor; it is absent in termites, parasitic lice, many Plecoptera, and most Ephemeroptera. Ovipositors take two forms:

1. true, or appendicular, formed from appendages of abdominal segments 8 and 9;
1. substitutional, composed of extensible posterior abdominal segments.

Other Appendages

Internal

Nervous system

The nervous system of an insect can be divided into a brain and a ventral nerve cord. The head capsule is made up of six fused segments, each with a pair of ganglia, or a cluster of nerve cells outside of the brain. The first three pairs of ganglia are fused into the brain, while the three following pairs are fused into a structure of three pairs of ganglia under the insect's esophagus, called the subesophageal ganglion.[1]:57

The thoracic segments have one ganglion on each side, which are connected into a pair, one pair per segment. This arrangement is also seen in the abdomen but only in the first eight segments. Many species of insects have reduced numbers of ganglia due to fusion or reduction.[42] Some cockroaches have just six ganglia in the abdomen, whereas the wasp *Vespa crabro* has only two in the thorax and three in the abdomen. Some insects, like the house fly *Musca domestica*, have all the body ganglia fused into a single large thoracic ganglion.

At least a few insects have nociceptors, cells that detect and transmit sensations of pain.[43] This was discovered in 2003 by studying the variation in reactions of larvae of the common fruitfly Drosophila to the touch of a heated probe and an unheated one. The larvae reacted to the touch of the heated probe with a stereotypical rolling behavior that was not exhibited when the larvae were touched by the unheated probe.[44] Although nociception has been demonstrated in insects, there is not a consensus that insects feel pain consciously.[45]

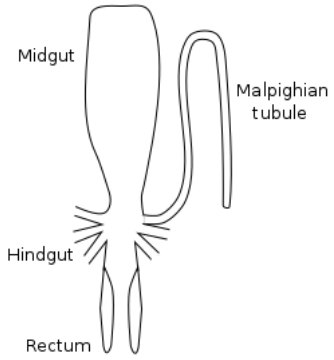
Digestive system

An insect uses its digestive system to extract nutrients and other substances from the food it consumes.[46] Most of this food is ingested in the form of macromolecules and other complex substances like proteins, polysaccharides, fats, and nucleic acids. These macromolecules must be broken down by catabolic reactions into smaller molecules like amino acids and simple sugars before being used by cells of the body for energy, growth, or reproduction. This break-down process is known as digestion. The main structure of an insect's digestive system is a long enclosed tube called the alimentary canal, which runs lengthwise through the body. The alimentary canal directs food in one direction: from the mouth to the anus. It has three sections, each of which performs a different process of digestion. In addition to the alimentary canal, insects also have paired salivary glands and salivary reservoirs. These structures usually reside in the thorax, adjacent to the foregut.[1]:70–77 The gut is where almost all of insects' digestion takes place. It can be divided into the foregut, midgut and hindgut.

Foregut

The first section of the alimentary canal is the foregut (element 27 in numbered diagram), or stomodaeum. The foregut is lined with a cuticular lining made of chitin and proteins as protection from tough food. The foregut includes the buccal cavity (mouth), pharynx, esophagus, and Crop and proventriculus (any part may be highly modified), which both store food and signify when to continue passing onward to the midgut.[1]:70 Here, digestion starts as partially chewed food is broken down by saliva from the salivary glands. As the salivary glands produce fluid and carbohydrate-digesting enzymes (mostly amylases), strong muscles in the pharynx pump fluid into the buccal cavity, lubricating the food like the salivarium does, and helping blood feeders, and xylem and phloem feeders.

From there, the pharynx passes food to the esophagus, which could be just a simple tube passing it on to the crop and proventriculus, and then on ward to the midgut, as in most insects. Alternately, the foregut may expand into a very enlarged crop and proventriculus, or the crop could just be a diverticulum, or fluid filled structure, as in some Diptera species.[47]:30–31



Stylized diagram of insect digestive tract showing malpighian tubule, from an insect of the order Orthoptera.

The salivary glands (element 30 in numbered diagram) in an insect's mouth produce saliva. The salivary ducts lead from the glands to the reservoirs and then forward through the head to an opening called the salivarium, located behind the hypopharynx. By moving its mouthparts (element 32 in numbered diagram) the insect can mix its food with saliva. The mixture of saliva and food then travels through the salivary tubes into the mouth, where it begins to break down.[46][48] Some insects, like flies, have extra-oral digestion. Insects using extra-oral digestion expel digestive enzymes onto their food to break it down. This strategy allows insects to extract a significant proportion of the available nutrients from the food source.[47]:31



Bumblebee defecating. Note the contraction of the anus, which provides internal pressure.

Midgut

Once food leaves the crop, it passes to the midgut (element 13 in numbered diagram), also known as the mesenteron, where the majority of digestion takes place. Microscopic projections from the midgut wall, called microvilli, increase the surface area of the wall and allow more nutrients to be absorbed; they tend to be close to the origin of the midgut. In some insects, the role of the microvilli and where they are located may vary. For example, specialized microvilli producing digestive enzymes may more likely be near the end of the midgut, and absorption near the origin or beginning of the midgut.[47]:32

Hindgut

In the hindgut (element 16 in numbered diagram), or proctodaeum, undigested food particles are joined by uric acid to form fecal pellets. The rectum absorbs 90% of the water in these fecal pellets, and the dry pellet is then eliminated through the anus (element 17), completing the process of digestion. The uric acid is formed using hemolymph waste products diffused from the Malpighian tubules (element 20). It is then emptied directly into the alimentary canal, at the junction between the midgut and hindgut. The number of Malpighian tubules possessed by a given insect varies between species, ranging from only two tubules in some insects to over 100 tubules in others.[1]:71–72, 78–80

Respiratory systems

Insect respiration is accomplished without lungs. Instead, the insect respiratory system uses a system of internal tubes and sacs through which gases either diffuse or are actively pumped, delivering oxygen directly to tissues that need it via their trachea (element 8 in numbered diagram). Since oxygen is delivered directly, the circulatory system is not used to carry oxygen, and is therefore greatly reduced. The insect circulatory system has no veins or arteries, and instead consists of little more than a single, perforated dorsal tube that pulses peristaltically. Toward the thorax, the dorsal tube (element 14) divides into chambers and acts like the insect's heart. The opposite end of the dorsal tube is like the aorta of the insect circulating the hemolymph, arthropods' fluid analog of blood, inside the body cavity.[1]:61–65[49] Air is taken in through openings on the sides of the abdomen called spiracles.

There are many different patterns of gas exchange demonstrated by different groups of insects. Gas exchange patterns in insects can range from continuous and diffusive ventilation, to discontinuous gas exchange.[1]:65–68 During continuous gas exchange, oxygen is taken in and carbon dioxide is released in a continuous cycle. In discontinuous gas exchange, however, the insect takes in oxygen while it is active and small amounts of carbon dioxide are released when the insect is at rest.[50] Diffusive ventilation is simply a form of continuous gas exchange that occurs by diffusion rather than physically taking in the oxygen. Some species of insect that are submerged also have adaptations to aid in respiration. As larvae, many insects have gills that can extract oxygen dissolved in water, while others need to rise to the water surface to replenish air supplies, which may be held or trapped in special structures.[51][52]

Circulatory system

Insect blood or haemolymph's main function is that of transport and it bathes the insect's body organs. Making up usually less than 25% of an insect's body weight, it transports hormones, nutrients and wastes and has a role in, osmoregulation, temperature control, immunity, storage (water, carbohydrates and fats) and skeletal function. It also plays an essential part in the moulting process.[53][54] An additional role of the haemolymph in some orders, can be that of predatory defence. It can contain unpalatable and malodourous chemicals that will act as a deterrent to predators.[1] Haemolymph contains molecules, ions and cells;[1] regulating chemical exchanges between tissues, haemolymph is encased in the insect body cavity or haemocoel.[1][55] It is transported around the body by combined heart (posterior) and aorta (anterior) pulsations, which are located dorsally just under the surface of the body.[1][53][54] It differs from vertebrate blood in that it doesn't contain any red blood cells and therefore is without high oxygen carrying capacity, and is more similar to lymph found in vertebrates.[1][55]

Body fluids enter through one-way valved ostia, which are openings situated along the length of the combined aorta and heart organ. Pumping of the haemolymph occurs by waves of peristaltic contraction, originating at the body's posterior end, pumping forwards into the dorsal vessel, out via the aorta and then into the head where it flows out into the haemocoel.[1][55] The haemolymph is circulated to the appendages unidirectionally with the aid of muscular pumps or accessory pulsatile organs usually found at the base of the antennae or wings and sometimes in the legs,[1] with pumping rates accelerating with periods of increased activity.[54] Movement of haemolymph is particularly important for thermoregulation in orders such as Odonata, Lepidoptera, Hymenoptera and Diptera.[1]

Endocrine system

These glands are part of the endocrine system:

1. Neurosecretory cells

2. Corpora cardiaca

3. Prothoracic glands

4. Corpora allata[56][57]

Reproductive system

Female

Female insects are able make eggs, receive and store sperm, manipulate sperm from different males, and lay eggs. Their reproductive systems are made up of a pair of ovaries, accessory glands, one or more spermathecae, and ducts connecting these parts. The ovaries make eggs and accessory glands produce the substances to help package and lay the eggs. Spermathecae store sperm for varying periods of time and, along with portions of the oviducts, can control sperm use. The ducts and spermathecae are lined with a cuticle.[8]:880

The ovaries are made up of a number of egg tubes, called ovarioles, which vary in size and number by species. The number of eggs that the insect is able to make vary by the number of ovarioles with the rate that eggs can be developed being also influenced by ovariole design. In meroistic ovaries, the eggs-to-be divide repeatedly and most of the daughter cells become helper cells for a single oocyte in the cluster. In panoistic ovaries, each egg-to-be produced by stem germ cells develops into an oocyte; there are no helper cells from the germ line. Production of eggs by panoistic ovaries tends to be slower than that by meroistic ovaries.[8]:880

Accessory glands or glandular parts of the oviducts produce a variety of substances for sperm maintenance, transport, and fertilization, as well as for protection of eggs. They can produce glue and protective substances for coating eggs or tough coverings for a batch of eggs called oothecae. Spermathecae are tubes or sacs in which sperm can be stored between the time of mating and the time an egg is fertilized. Paternity testing of insects has revealed that some, and probably many, female insects use the spermatheca and various ducts to control or bias sperm used in favor of some males over others.[8]:880

Male

The main component of the male reproductive system is the testis, suspended in the body cavity by tracheae and the fat body. The more primitive apterygote insects have a single testis, and in some lepidopterans the two maturing testes are secondarily fused into one structure during the later stages of larval development, although the ducts leading from them remain separate. However, most male insects have a pair of testes, inside of which are sperm tubes or follicles that are enclosed within a membranous sac. The follicles connect to the vas deferens by the vas efferens, and the two tubular vasa deferentia connect to a median ejaculatory duct that leads to the outside. A portion of the vas deferens is often enlarged to form the seminal vesicle, which stores the sperm before they are discharged into the female. The seminal vesicles have glandular linings that secrete nutrients for nourishment and maintenance of the sperm. The ejaculatory duct is derived from an invagination of the epidermal cells during development and, as a result, has a cuticular lining. The terminal portion of the ejaculatory duct may be sclerotized to form the intromittent organ, the aedeagus. The remainder of the male reproductive system is derived from embryonic mesoderm, except for the germ cells, or spermatogonia, which descend from the primordial pole cells very early during embryogenesis.[8]:885 The aedeagus can be quite pronounced or *de minimis*. The base of the aedeagus may be the partially sclerotized phallotheca, also called the phallosoma or theca. In some species the phallotheca contains a space, called the endosoma (internal holding pouch), into which the tip end of the aedeagus may be withdrawn (retracted). The vas deferens is sometimes drawn into (folded into) the phallotheca together with a seminal vesicle.[58][59]

Internal morphology of different taxa

Blattodea

Cockroaches are most common in tropical and subtropical climates. Some species are in close association with human dwellings and widely found around garbage or in the kitchen. Cockroaches are generally omnivorous with the exception of the wood-eating species such as *Cryptocercus*; these roaches are incapable of digesting cellulose themselves, but have symbiotic relationships with various protozoans and bacteria that digest the cellulose, allowing them to extract the nutrients. The similarity of these symbionts in the genus *Cryptocercus* to those in termites are such that it has been suggested that they are more closely related to termites than to other cockroaches,[60] and current research strongly supports this hypothesis of relationships.[61] All species studied so far carry the obligate mutualistic endosymbiont bacterium *Blattabacterium*, with the exception of *Nocticola australiensis*, an Australian cave dwelling species without eyes, pigment or wings, and which recent genetic studies indicates are very primitive cockroaches.[62][63]

Cockroaches, like all insects, breathe through a system of tubes called *tracheae*. The tracheae of insects are attached to the spiracles, excluding the head. Thus cockroaches, like all insects, are not dependent on the mouth and windpipe to breathe. The valves open when the CO_2 level in the insect rises to a high level; then the CO_2 diffuses out of the tracheae to the outside and fresh O_2 diffuses in. Unlike in vertebrates that depend on blood for transporting O_2 and CO_2, the tracheal system brings the air directly to cells, the tracheal tubes branching continually like a tree until their finest divisions, tracheoles, are associated with each cell, allowing gaseous oxygen to dissolve in the cytoplasm lying across the fine cuticle lining of the tracheole. CO_2 diffuses out of the cell into the tracheole. While cockroaches do not have lungs and thus do not actively breathe in the vertebrate lung manner, in some very large species the body musculature may contract rhythmically to forcibly move air out and in the spiracles; this may be considered a form of breathing.[64]

Coleoptera

The digestive system of beetles is primarily based on plants, which they for the most part feed upon, with mostly the anterior midgut performing digestion. However, in predatory species (e.g., Carabidae) most digestion occurs in the crop by means of midgut enzymes. In Elateridae species, the predatory larvae defecate enzymes on their prey, with digestion being extraorally.[8] The alimentary canal basically comprises a short narrow pharynx, a widened expansion, the crop and a poorly developed gizzard. After there is a midgut, that varies in dimensions between species, with a large amount of cecum, with a hingut, with varying lengths. There are typically four to six Malpighian tubules.[65]

The nervous system in beetles contains all the types found in insects, varying between different species. With three thoracic and seven or eight abdominal ganglia can be distinguished to that in which all the thoracic and abdominal ganglia are fused to form a composite structure. Oxygen is obtained via a tracheal system. Air enters a series of tubes along the body through openings called spiracles, and is then taken into increasingly finer fibers.[8] Pumping movements of the body force the air through the system. Some species of diving beetles (**Dytiscidae**) carry a bubble of air with them whenever they dive beneath the water surface. This bubble may be held under the elytra or it may be trapped against the body using specialized hairs. The bubble usually covers one or more spiracles so the insect can breathe air from the bubble while submerged. An air bubble provides an insect with only a short-term supply of oxygen, but thanks to its unique physical properties, oxygen will diffuse into the bubble and displacing the nitrogen, called passive diffusion, however the volume of the bubble eventually diminishes and the beetle will have to return to the surface.[66]

Like other insect species, beetles have hemolymph instead of blood. The open circulatory system of the beetle is driven by a tube-like heart attached to the top inside of the thorax.

Different glands specialize for different pheromones produced for finding mates. Pheromones from species of Rutelinea are produced from epithelial cells lining the inner surface of the apical abdominal segments or amino acid based pheromones of Melolonthinae from eversible glands on the abdominal apex. Other species produce different types of pheromones. Dermestids produce esters, and species of Elateridae produce fatty-acid-derived aldehydes and acetates.[8] For means of finding a mate also, fireflies (Lampyridae) utilized modified fat body cells with transparent surfaces backed with reflective uric acid crystals to biosynthetically produce light, or bioluminescence. The light produce is highly efficient, as it is produced by oxidation of luciferin by the enzymes luciferase in the presence of ATP (adenosine triphospate) and oxygen, producing oxyluciferin, carbon dioxide, and light.[8]

A notable number of species have developed special glands that produce chemicals for deterring predators (see Defense and predation). The Ground beetle's (of Carabidae) defensive glands, located at the posterior, produce a variety of hydrocarbons, aldehydes, phenols, quinones, esters, and acids released from an opening at the end of the abdomen. While African carabid beetles (e.g., *Anthia* some of which used to comprise the genus *Thermophilum*) employ the same chemicals as ants: formic acid.[31] While Bombardier beetles have well developed, like other carabid beetles, pygidial glands that empty from the lateral edges of the intersegment membranes between the seventh and eighth abdominal segments. The gland is made of two containing chambers. The first holds hydroquinones and hydrogen peroxide, with the second holding just hydrogen peroxide plus catalases. These chemicals mix and result in an explosive ejection, forming temperatures of around 100 C, with the breakdown of hydroquinone to $H_2 + O_2$ + quinone, with the O_2 propelling the excretion.[8]

Tympanal organs are hearing organs. Such an organ is generally a membrane (tympanum) stretched across a frame backed by an air sac and associated sensory neurons. In the order Coleoptera, tympanal organs have been described in at least two families.[30] Several species of the genus *Cicindela* in the family **Cicindelidae** have ears on the dorsal surface of the first abdominal segment beneath the wing; two tribes in the family Dynastinae (**Scarabaeidae**) have ears just beneath the pronotal shield or neck membrane. The ears of both families are to ultrasonic frequencies, with

strong evidence that they function to detect the presence of bats via their ultrasonic echolocation. Even though beetles constitute a large order and live in a variety of niches, examples of hearing is surprisingly lacking in species, though it is likely that most are just undiscovered.[8]

Dermaptera

The neuroendocrine system is typical of insects. There is a brain, a subesophageal ganglion, three thoracic ganglia, and six abdominal ganglia. Strong neuron connections connect the neurohemal corpora cardiaca to the brain and frontal ganglion, where the closely related median corpus allatum produces juvenile hormone III in close proximity to the neurohemal dorsal aorta. The digestive system of earwigs is like all other insects, consisting of a fore-, mid-, and hindgut, but earwigs lack gastric caecae which are specialized for digestion in many species of insect. Long, slender (extratory) malpighian tubules can be found between the junction of the mid- and hind gut.[8]

The reproductive system of females consist of paired ovaries, lateral oviducts, spermatheca, and a genital chamber. The lateral ducts are where the eggs leave the body, while the spermatheca is where sperm is stored. Unlike other insects, the gonopore, or genital opening is behind the seventh abdominal segment. The ovaries are primitive in that they are polytrophic (the nurse cells and oocytes alternate along the length of the ovariole). In some species these long ovarioles branch off the lateral duct, while in others, short ovarioles appear around the duct.[8]

Diptera

The genitalia of female flies are rotated to a varying degree from the position found in other insects. In some flies this is a temporary rotation during mating, but in others it is a permanent torsion of the organs that occurs during the pupal stage. This torsion may lead to the anus being located below the genitals, or, in the case of 360° torsion, to the sperm duct being wrapped around the gut, despite the external organs being in their usual position. When flies mate, the male initially flies on top of the female, facing in the same direction, but then turns round to face in the opposite direction. This forces the male to lie on its back in order for its genitalia to remain engaged with those of the female, or the torsion of the male genitals allows the male to mate while remaining upright. This leads to flies having more reproduction abilities than most insects and at a much quicker rate. Flies come in great populations due to their ability to mate effectively and in a short period of time especially during the mating season.[67]

The female lays her eggs as close to the food source as possible, and development is very rapid, allowing the larva to consume as much food as possible in a short period of time before transforming into the adult. The eggs hatch immediately after being laid, or the flies are ovoviviparous, with the larva hatching inside the mother.[67] Larval flies, or maggots, have no true legs, and little demarcation between the thorax and abdomen; in the more derived species, the head is not clearly distinguishable from the rest of the body. Maggots are limbless, or else have small prolegs. The eyes and antennae are reduced or absent, and the abdomen also lacks appendages such as cerci. This lack of features is an adaptation to a food-rich environment, such as within rotting organic matter, or as an endoparasite.[67] The pupae take various forms, and in some cases develop inside a silk cocoon. After emerging from the pupa, the adult fly rarely lives more than a few days, and serves mainly to reproduce and to disperse in search of new food sources.

Lepidoptera

In reproductive system of butterflies and moths, the male genitalia are complex and unclear. In females there are three types of genitalia based on the relating taxa: monotrysian, exoporian, and dytresian. In the monotrysian type there is an opening on the fused segments of the sterna 9 and 10, which act as insemination and oviposition. In the exoporian type (in Hepaloidae and Mnesarchaeoidea) there are two separate places for insemination and oviposition, both occurring on the same sterna as the monotrysian type, 9/10. In most species the genitalia are flanked by two soft lobes, although they may be specialized and sclerotized in some species for ovipositing in area such as crevices and inside plant tissue.[65] Hormones and the glands that produce them run the development of butterflies and moths as they go through their life cycle, called the endocrine system. The first insect hormone PTTH (Prothoracicotropic hormone) operates the species life cycle and diapause (see the relates section).[68] This hormone is produced by corpora allata and corpora cardiaca, where it is also stored. Some glands are specialized to perform certain task such as producing silk or producing saliva in the palpi.[1]:65, 75 While the corpora cardiaca produce PTTH, the corpora allata also produces jeuvanile hormones, and the prothorocic glands produce moulting hormones.

In the digestive system, the anterior region of the foregut has been modified to form a pharyngial sucking pump as they need it for the food they eat, which are for the most part liquids. An esophagus follows and leads to the posterior of the pharynx and in some species forms a form of crop. The midgut is short and straight, with the hindgut being longer and coiled.[65] Ancestors of lepidopteran species, stemming from Hymenoptera, had midgut ceca, although this is lost in current butterflies and moths. Instead, all the digestive enzymes other than initial digestion, are immobilized at the surface of the midgut cells. In larvae, long-necked and stalked goblet cells are found in the anterior and posterior midgut regions, respectively. In insects, the goblet cells excrete positive potassium ions, which are absorbed from leaves ingested by the larvae. Most butterflies and moths display the usual digestive cycle, however species that have a different diet require adaptations to meet these new demands.[8]:279

In the circulatory system, hemolymph, or insect blood, is used to circulate heat in a form of thermoregulation, where muscles contraction produces heat, which is transferred to the rest of the body when conditions are unfavorable.[69] In lepidopteran species, hemolymph is circulated through the veins in the wings by some form of pulsating organ, either by the heart or by the intake of air into the trachea.[1]:69 Air is taken in through spiracles along the sides of the abdomen and thorax supplying the trachea with oxygen as it goes through the lepidopteran's respiratory system. There are three different tracheae supplying oxygen diffusing oxygen throughout the species body: The dorsal, ventral, and visceral. The dorsal tracheae supply oxygen to the dorsal musculature and vessels, while the ventral tracheae supply the ventral musculature and nerve cord, and the visceral tracheae supply the guts, fat bodies, and gonads.[1]:71, 72

See also

- Morphology (biology)
- Insect physiology
- External morphology of Lepidoptera
- External morphology of Odonata
- Insect ecology
- Insect flight
- Invertebrate
- Insect
- Entomology
- Prehistoric insect

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